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A remarkable group of thick-headed Triassic Period archosauromorphs with a wide, possibly Pangean distribution

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Abstract

The radiation of archosauromorph reptiles in the Triassic Period produced an unprecedented collection of diverse and disparate forms with a mix of varied ecologies and body sizes. Some of these forms were completely unique to the Triassic, whereas others were converged on by later members of Archosauromorpha. One of the most striking examples of this is with *Triopticus primus*, the early dome-headed form later mimicked by pachycephalosaurid dinosaurs. Here we fully describe the cranial anatomy of *Triopticus primus*, but also recognize a second dome-headed form from a Upper Triassic deposit in present-day India. The new taxon, *Kranosaura kuttyi* gen. et sp. nov., is likely the sister taxon of *Triopticus primus* based on the presence of a greatly expanded skull roof with a deep dorsal opening (possibly the pineal opening) through the dome, similar cranial sculpturing, and a skull table that is expanded more posterior than the posterior extent of the basioccipital. However, the dome of *Kranosaura kuttyi* gen. et sp. nov. extends anterodorsally, unlike that of any other archosauromorph. Histological sections and computed tomographic reconstructions through the skull of *Kranosaura kuttyi* gen. et sp. nov. further reveal the uniqueness of the dome of these early archosauromorphs. Moreover, our integrated analysis further demonstrates that there are many ways to create a dome in Amniota. The presence of 'dome-headed' archosauromorphs at two localities on the western and eastern portions of Pangea suggests that these archosauromorphs were widespread and are likely part of more assemblages than currently recognized.

KEYWORDS
Archosauromorpha, convergence, late Triassic, Maleri Formation, Pachycephalosauria

1 | INTRODUCTION

The Triassic Period has been recognized as a time of the proliferation of disparate body plans following the end-Permian mass extinction (Benton, 1985; Fraser, 2006; Sues & Fraser, 2010), with a wide morphospace established by archosauromorphs by the Late Triassic (Foth et al., 2016; Sengupta et al., 2017; Stocker et al., 2016). Those explorations of morphospace represent not just taxonomic diversification but also diversification into novel ecological roles, with many morphologies having been interpreted as indicators of specific paleoecologies (explosion of herbivory; Crompton & Attridge, 1986; Dzik, 2003; Parker et al., 2005; Barrett et al., 2011; the 'aquatic carnivore' morphotype exemplified by phytosaurs; Colbert, 1947; Stocker & Butler, 2013; Lessner & Stocker, 2017). This range of body plans present in the Triassic is found within taxa whose external morphology, either superficially or sometimes in great detail, is most often repeated later in the Mesozoic by dinosaurs once these earlier forms go extinct (Stocker et al., 2016).

One of the best assemblages documenting this Triassic morphospace occupation prior to later Mesozoic convergence is that from the Otis Chalk localities in Texas, USA (Stocker et al., 2016). One of the most extraordinary taxa described from that assemblage is the archosauriform *Triopticus primus*, whose cranial morphology was superficially mimicked by Cretaceous pachycephalosaur dinosaurs. *Triopticus* and pachycephalosaurs share a dorsoventrally thickened skull roof, a posteriorly expanded and thickened posterior margin of the skull with bony nodes, and enlarged orbits. In addition to gross morphological similarities, those taxa also share a tripartite histological construction to that thickened 'dome' of the skull roof with three 'zones' of bone growth with varying degrees of porosity and vascularity (Stocker et al., 2016).

Here, we describe a new archosauriform from the Upper Triassic Upper Maleri Formation of India and propose that this new taxon is closely related to the similarly-domed *Triopticus primus* of present-day Texas, USA. We fully describe each taxon in a comparative framework and demonstrate the previously proposed anatomical convergences among the Triassic forms and Cretaceous pachycephalosaur dinosaurs, based on the morphology of the external features, are misleading once histological features of the dorsal skull expansion are fully taken into consideration.

Institutional Abbreviations—ISI, Indian Statistical Institute, Kolkata, India; TMM, Texas Vertebrate Paleontology Collections, The University of Texas at Austin, Texas, USA; UALVP, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada.

2 | MATERIALS AND METHODS

2.1 | Histology

Five histological thin sections were taken from ISIR 268 (Figure 10): two full length sagittal sections and three transverse sections. Slides were sectioned in the Gabriel Laboratory for Cellular and Molecular Paleontology at the Museum of the Rockies, Montana State University, Bozeman, MT, USA, by Ms. Ellen Lamm in accordance with published techniques (see Lamm, 2013). The sections were examined and photographed using a Nikon Eclipse E600 POL microscope under plane, condensed, and cross-polarized light (with 2× to 50× objectives) using a lambda compensator, and a Nikon Digital Sight DS-L1 camera. Images with a bluish tint were photographed through an NCB11 white balance filter to provide high contrast. Most of the images were taken after the specimens had been wetted (H_2O).

2.2 | Computed tomography (CT)

ISIR 268 and ISIR 269 were scanned in November 2007 at Bozeman Deaconess Hospital - Computed Tomography (CT) facility (now American Advanced Imaging [AMI], part of the Bozeman Deaconess Hospital complex) by radiology technician Katie Ugrin. Scans were made using a Marconi M8000 Multislice machine at 140 kV and 257 mA, with a 3.0 mm slice thickness and 0.1432 mm interpixel spacing. We then processed the reconstructed images with Mimics (Materialise) version 19 software.

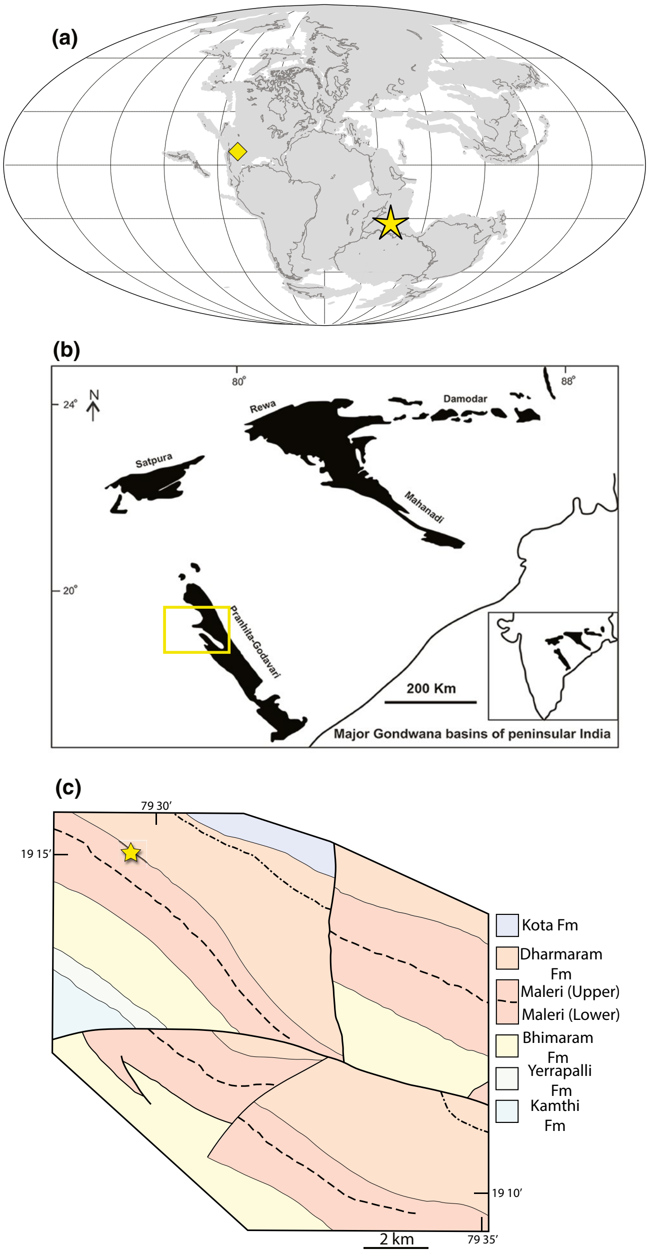


FIGURE 1 Distribution of Protopyknosia. (a) Paleomap depicting continental arrangements in the Late Triassic. Diamond indicates the Colorado City Formation in Texas, the type locality of *Triopticus primus*, and star indicates the Upper Maleri Formation in India, the type locality of *Kranosaura kuttyi*. (b) Overview of the Gondwanan basins in India, with the Pranhita-Godavari valley highlighted. Modified from Sengupta et al. (2017). (c) Detailed plan view geological map indicating the type locality of *Kranosaura kuttyi* within the Upper Maleri Formation. Modified from Kutty and Sengupta (1989)

2.3 | Nomenclatural Acts

This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the International Code of Zoological Nomenclature. The ZooBank Life Science Identifiers (LSIDs) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://www.zoobank.org/. The LSIDs for this publication are as follows: urn:lsid:zoobank.org:pub:D02FB4FB-B406-4BFF-85A5-466815B19C58 (publication); urn:lsid:zoobank.org:act:02361C7A-51A7-4274-9FA9-6142829C65F0 (genus); urn:lsid:zoobank.org:act:A4F807C5-15C8-4E92-BB1D-7799A75CD2C3 (species).

2.3.1 | Data availability

The reconstructed images for both specimens and reconstructed surface meshes of *Kranosaura kuttyi* are openly available through Morphosource.org. We also used the original CT dataset of *Triopticus primus* scanned using the parameters detailed by Stocker et al. (2016), which is also openly available through Morphosource.org under project P181. The holotype of *Triopticus primus* is held at the Texas Vertebrate Paleontology Collections, The University of Texas at Austin, Texas, USA, and the holotype and referred specimen of *Kranosaura kuttyi* gen. et sp. nov. is held at the paleontological collections of the Indian Statistical Institute, Kolkata, India.

2.3.2 | Systematic paleontology

Reptilia Laurenti, 1768.

Archosauromorpha Huene, 1946 sensu Benton, 1985.

Archosauriformes Gauthier et al., 1988.

Protopyknosia clade nov.

Etymology – From the Greek "proto" (original) and "pyknos" (thick) referring to the early appearance of an extensively expanded top of the skull in these reptiles.

Diagnosis – Protopyknosia differs from all other archosauromorphs in possessing the following unique combination of character states: deep pit in posterodorsal surface of skull, posterior to the orbits; slightly rugose lateral and posterior portions of skull roof; enlarged, highly ossified dorsal region of skull; lateral surfaces of the dorsal expansion medially excavated dorsal to the posterior portion of orbit; fused circumorbital elements; posterior edge of skull table expanded well posterior of the posterior extent of the basioccipital.

Additional character states present in *Triopticus primus*, but unknown in *Kranosaura kuttyi* include: large posttemporal fenestrae; horizontally-oriented parabasisphenoid; ossified laterosphenoid that divides orbits; ventral projection on the midline of basioccipital.

Definition – The most inclusive clade containing *Triopticus primus* Stocker et al., 2016, but not *Passer domesticus* Linnaeus, 1758, *Triceratops horridus* (Marsh, 1889), *Alligator mississippiensis* Daudin, 1801, *Sphenodon punctatus* Gray, 1842, *Heloderma suspectum* Cope, 1869, or *Chrysemys picta* (Schneider, 1783).

Kranosaura kuttyi gen. et sp. nov.

Etymology – From the Greek 'Kranos' (helmet) and 'saura' (lizard or reptile) referring to the large expansion on the top of the head of this reptile. The specific name honors T. S. Kutty, who discovered the material.

Holotype – ISIR 269, dorsal portion of the skull (Figures 2 and 5).

Locality and age – Upper Maleri Formation, Pranhita-Godavari Valley, Deccan, India (Figure 1). 79°29.5′E 19°15′N. Other tetrapod taxa from the Upper Maleri Formation include: the sauropodomorphs *Nambalia roychowdhurii* and *Jaklapallisaurus asymmetrica*, a member of Guaibasauridae, and other dinosaur remains (Novas et al., 2011); phytosaurs (Sengupta, 1995; Hungerbühler et al., 2002) similar to the North American genera *Angistorhinus* and *Leptosuchus*, equivalent to the 'advanced phytosaur zone' of Chatterjee (1986); the chugutisaurid temnospondyls *Compsocerops cosgriffi* and *Kuttycephalus triangularis* (Sengupta, 1995); dicynodonts and aetosaurs (Bandyopadhyay & Sengupta, 2006; Kutty & Sengupta, 1989). The Upper Maleri fauna suggests a Late Triassic (Norian) age and Adamanian holochronozone and is correlated with the Bull Canyon Formation of the Dockum Group of North America (Chatterjee et al., 2017). In contrast, *Triopticus* was described from the older Colorado City Formation of the Dockum Group of latest Carnian–earliest Norian (Otischalkian biozone) age (Stocker et al., 2016).

Diagnosis – *Kranosaura kuttyi* possesses all of the character states present in Protopyknosia and can be further differentiated from *Triopticus primus* by the possession of the following combintation of character states: larger expansion of dorsal surface of the skull and greater anterior expansion of 'dome'; dorsal surface of skull covered in evenly-distributed foramina across the dorsalmost expansion; relative expansion of 'postorbital region' less laterally expanded; expansion of 'squamosal region' extends further ventrally; less differentiation between 'postorbital region' and 'squamosal region' (these regions are continuous without a gap); deep pit in posterodorsal surface of skull proportionally smaller and directed more posteriorly.

Referred specimen – ISIR 268, anterodorsal portion of the skull including the 'frontal region', the anterior edge of the deep pit in the posterodorsal surface of the skull, and ventrally, the roof of the braincase (Figures 3–5 and 10–12). We refer ISIR 268 to *Kranosaura kuttyi* based on the presence of the following character states present in the holotype: small deep pit in posterodorsal surface of skull, large expansion of the dorsal surface of the skull into a highly rounded surface; dorsal surface of skull covered in evenly-distributed foramina across the dorsalmost expansion; lateral sides of the dorsal expansion medially excavated dorsal to the orbits. Furthermore, ISIR 268 was discovered at the holotype locality.

2.4 | Description of the anatomy of Protopyknosia

General – The partial skull and only known specimen of *Triopticus primus* (Figures 6–9) consists of the skull table from the sutural contact with the nasal(s) posterior to the posterior edge of the parietals, postorbital/postfrontal and squamosal regions, much of the orbital region, the dorsal head of the left quadrate, a nearly complete braincase missing part of the right side, palatal elements including a partial pterygoid and elements possibly pertaining to the palatines, and a fragment of the left lacrimal. *Kranosaura kuttyi* consists of two specimens (ISIR 268, 269; Figures 2–5), of which the holotype (ISIR 269; Figures 2 and 5) is more complete, and the referred specimen (ISIR 268; Figures 3–5) almost completely overlaps the preserved morphology of the holotype except in the anteriormost portion of referred specimen (see below). The holotype of *Kranosaura kuttyi* (ISIR 269) consists of much of the expanded 'dome' including most of the frontals to the posterior edge of the partials, postorbital/postfrontal (right side) and squamosal regions (both sides), part of the dorsalmost portion of the braincase that is poorly preserved, and part of the posterodorsal portion of the orbits. The orbital region and surrounding bones are much better preserved in *Triopticus* than in *Kranosaura kuttyi*.

In general proportions, *Triopticus primus* and *Kranosaura kuttyi* share similarities in the large dorsal expansion of the skull table (see diagnosis above), but it is worth noting that the absolute size of *Kranosaura kuttyi* is larger than the holotype of *Triopticus*. Between the two specimens of *Kranosaura kuttyi*, the referred specimen (ISIR 268) is about 10-15% larger than the holotype.

The dorsal, posterior, and lateral surfaces of the skulls of *Triopticus primus* and *Kranosaura kuttyi* (Figures 2–9) are slightly rugose textured, but there are a few differences between the two taxa. First, the external surfaces of *Triopticus primus* are not as well-preserved as those of *Kranosaura kuttyi*. Second, the external surfaces of *Triopticus primus* lack the consistent pattern of small (0.5-3.0 mm in diameter), rounded, low protuberances present on the external surfaces of the skull table of the holotype of *Kranosaura kuttyi* (ISIR 269), whereas *Triopticus primus* has similar protuberances on the posterior portion of the squamosal region that are much more expanded from the rest of the surface of the skull. Third, both specimens of *Kranosaura kuttyi* have defined and regularly distributed foramina that cover much of the external surfaces. These foramina extend deep into the skull table elements (see histology section below).

Skull table – The skull table, consisting of coossified parietal, squamosal, postorbital, and frontal regions, is present in both *Triopticus primus* and *Kranosaura kuttyi* (Figures 2–9). Sutures between these

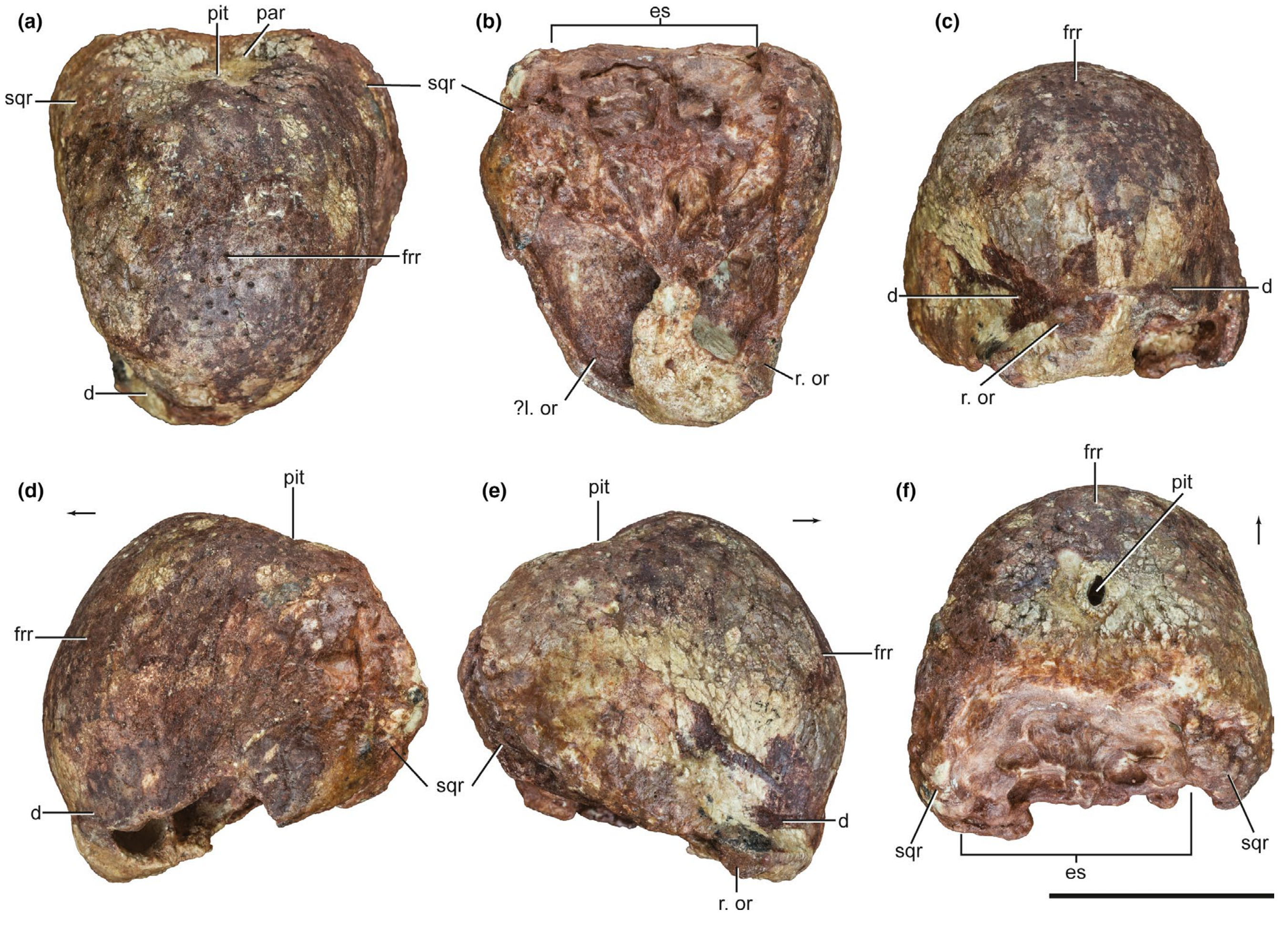


FIGURE 2 The holotype of *Kranosaura kuttyi* (ISIR 269) in (a) anterior, (b) posteroventral, (c) anteroventral, (d) left lateral, (e) right lateral, and (f) posterodorsal views. ?, unknown; d, depression; es, eroded surface; frr, frontal region; l., left; par, parietal region; pit, dorsal pit; or, orbit; r., right; sqr, squamosal region; stf, supratemporal fenestra. Arrows indicate anterior direction. Scale bar = 5 cm

skull roof elements of *Kranosaura kuttyi* are not clear internally or externally, as in *Triopticus* (Stocker et al., 2016). The frontal region is highly inflated dorsomedial to the orbits. In *Triopticus*, the anterior part of the dorsal expansion is slightly flatter anterodorsally than the gently rounded surface of *Kranosaura kuttyi*. Furthermore, the anteriormost portion of the frontal region in *Kranosaura kuttyi* is nearly vertical, whereas the same region in *Triopticus* is sloped at ~60-70° with the braincase oriented horizontally in the anteroposterior plane (Figure 5). The anteriormost portion of the preserved part of the skull of *Kranosaura kuttyi* is deflected dorsally in the referred specimen (ISIR 268) and slightly dorsally in the holotype (ISIR 269), whereas the same region in *Triopticus primus* appears to continue on the same slope where it presumably met the nasals, although this area is slightly broken. More laterally, small anteriorly and laterally expanded bosses mark the anterodorsal edge of the orbit in *Triopticus primus*. The bosses are more defined posterodorsally, and these bosses may represent the prefrontal.

The lateral sides of the dorsal 'dome' of the frontal region expand laterally (Figures 2–9) to roof a broad depression between the dorsal margin of the orbit and the dorsolateral portion of the dome in Protopyknosia. This lateral expansion (Figures 2 and 3) is more obvious in anterior view in *Kranosaura kuttyi* than in *Triopticus primus* (Figure 6) largely because the 'dome' of *Kranosaura kuttyi* narrows anteriorly toward the midline, whereas the lateral portions of the 'dome' of *Triopticus* do not converge anteriorly. The orbital rim in *Triopticus primus* is thin dorsoventrally and forms a distinct orbital region in comparison with the right side of the referred specimen of *Kranosaura kuttyi* (ISIR 268). Moreover, the posterior orbital margin of *Kranosaura kuttyi* is poorly defined compared to *Triopticus*. In *Triopticus primus* a well-defined postorbital/postfrontal region is laterally separated from that of the orbital region (Figure 6), and a small, anteriorly-opening fossa is present at the junction between the postorbital/postfrontal region and frontal region, just dorsal to the orbital rim (Figure 6). In dorsal view, the frontal region of the 'dome' in *Kranosaura kuttyi* is relatively wider compared to the more posterior skull table elements, whereas the frontal region of the 'dome' of *Triopticus primus* is narrower compared to the more posterior skull table elements (Figure 6).

Posterior to the frontal region expansion, the skulls of *Kranosaura kuttyi* and *Triopticus primus* slope posteriorly from a peak that lies at the posterior margin of the orbit. In *Triopticus primus*, this posterior slope has a shallower angle (~45°) than that of *Kranosaura kuttyi*

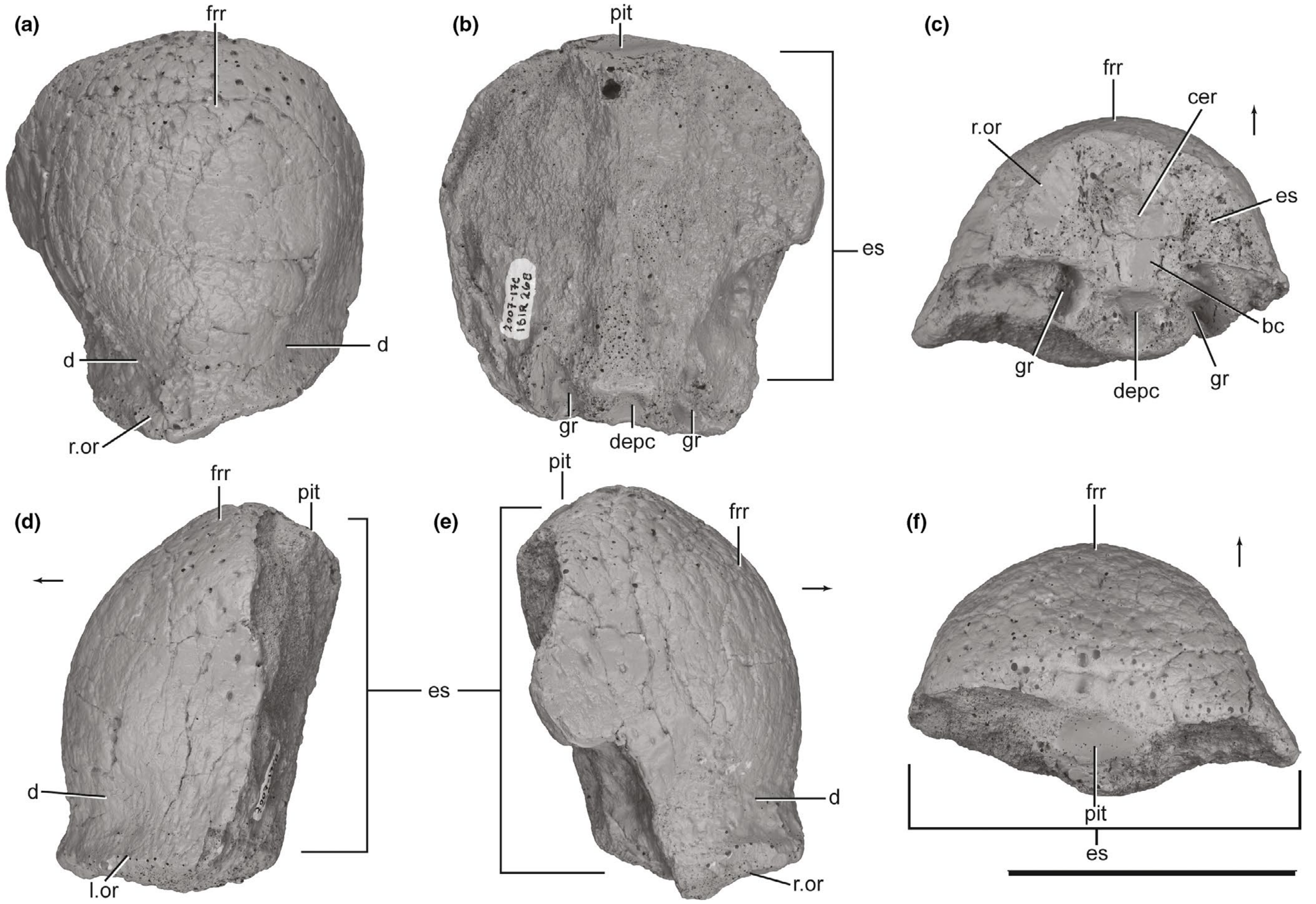


FIGURE 3 Cast of the referred specimen of *Kranosaura kuttyi* (ISIR 268) in (a) anterior, (b) posterior, (c) ventral, (d) left lateral, (e) right lateral, and (f) dorsal views. bc, dorsal surface of the endocast that caps the dorsal pit; cer, dorsal impression of the cerebrum; d, depression; dpec, dorsal surface of dural peak of the brain endocast; es, eroded surface; frr, frontal region; gr, groove; l., left; or, orbit; pit, dorsal pit; r., right. Arrows indicate anterior direction. Scale bar = 5 cm

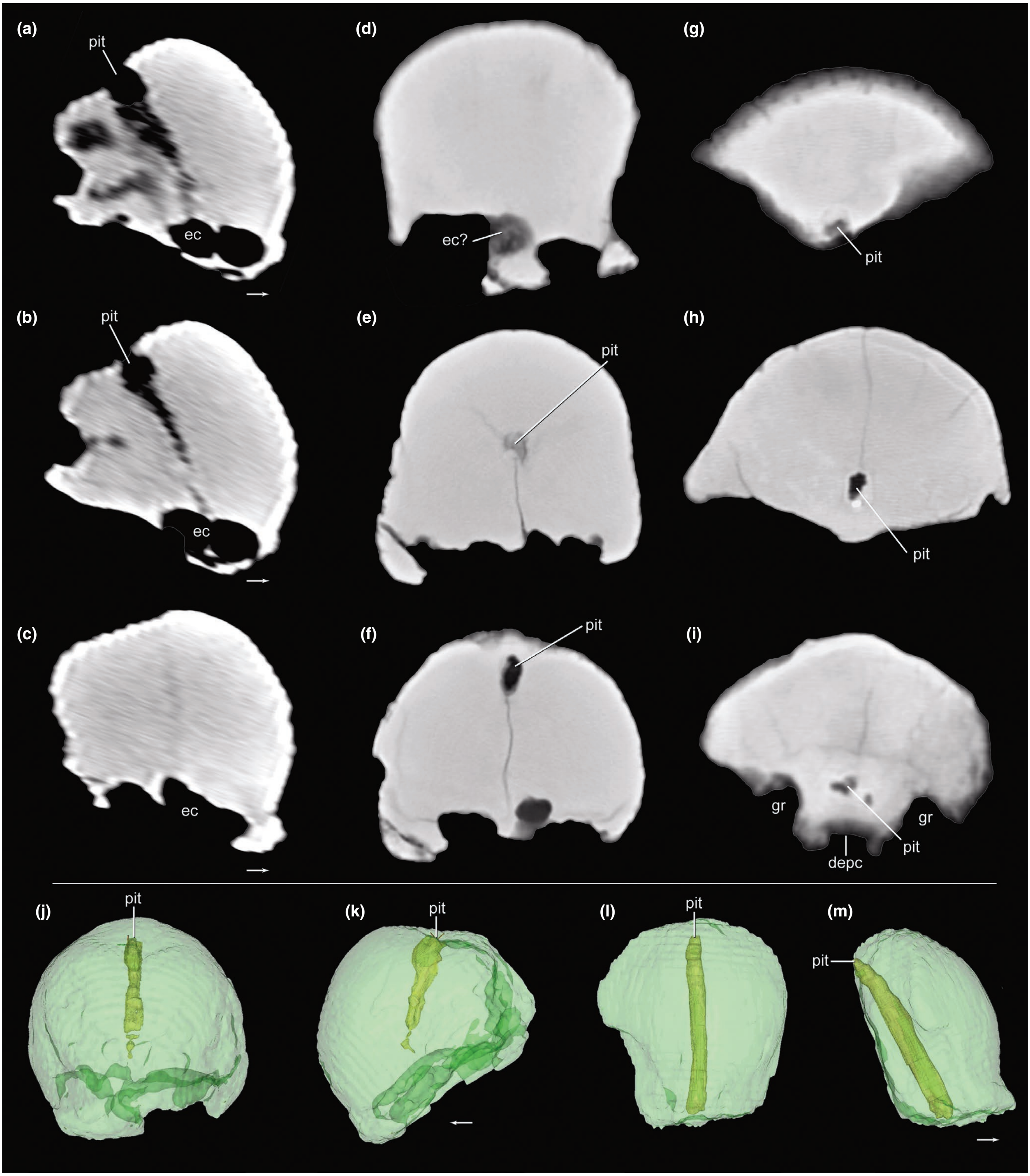


FIGURE 4 Reconstructed images and meshes of the holotype (ISIR 269) and referred specimen (ISIR 268) of *Kranosaura kuttyi*. Sagittal reconstructed images of ISIR 269 a–c starting at the center a and proceeding laterally to c Near coronal reconstructed images of ISIR 269 d-f starting anteroventrally d and proceeding posterodorsally to f. Transverse reconstructed images of ISIR 268 g-i starting dorsally g and proceeding ventrally to i. Transparent reconstructed mesh of ISIR 269 (green) illustrating the path of the dorsal pit (yellow) in anterior j and left lateral k views. Transparent reconstructed mesh of ISIR 268 (green) illustrating the path of the dorsal pit (yellow) in anterior j and right lateral K views. dpec, dorsal surface of dural peak of the brain endocast; ec, endocast; gr, groove; pit, dorsal pit. Arrows indicate anterior direction

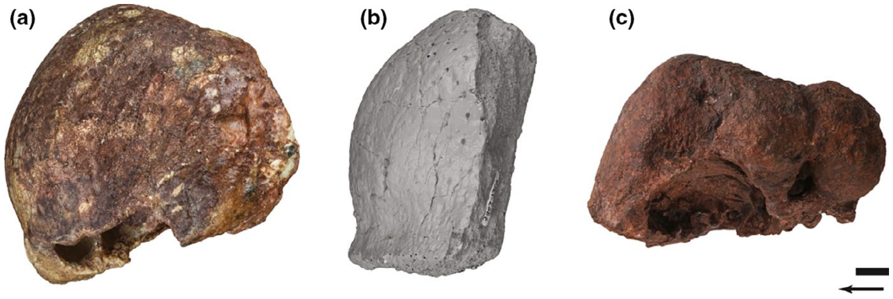


FIGURE 5 Skull orientation of the members of Protopyknosia. (a) Holotype of *Kranosaura kuttyi* (ISIR 269), (b) referred specimen of *Kranosaura kuttyi* (ISIR 268), and (c) *Triopticus primus* (TMM 31100-1030) in left lateral views. Arrow indicates anterior direction. Scale bar = 1 cm

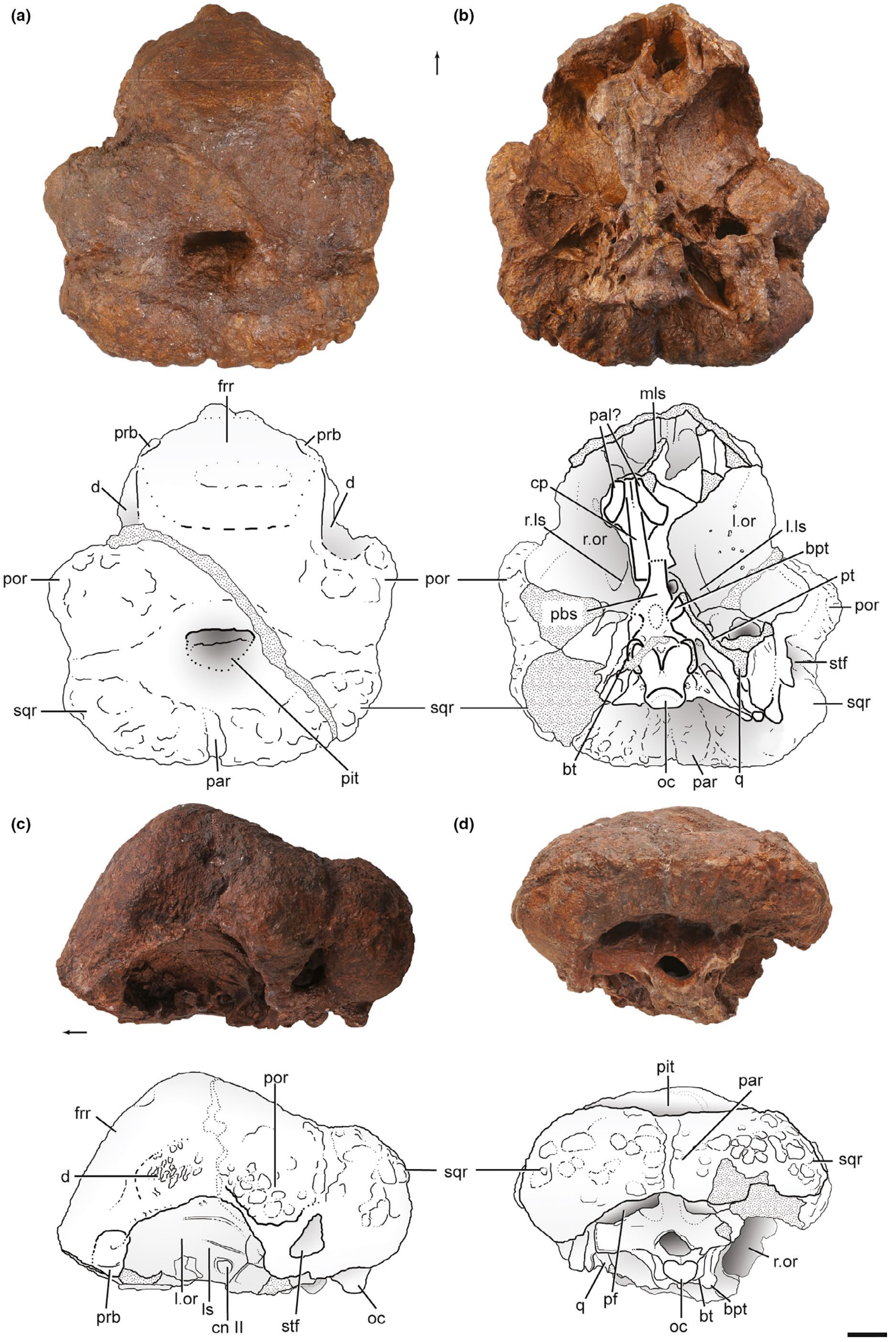
(~60°). At the midline, both *Kranosaura kuttyi* and *Triopticus primus* possess a dorsal opening; in *Triopticus primus*, the opening is directly dorsal to the posterior edge of the occipital condyle. The homology of this opening (=median pit in skull roof; see histology below) to the morphology of the skulls of other amniotes is unclear (see Stocker et al., 2016); it could be homologous to the parietal/pineal foramen of amniotes given its position, but the opening is not connected with the dorsal surface of the endocast. Furthermore, the bizarre morphology of the opening does not match that of any other known amniote.

Regardless, the morphology of the dorsal openings and the surrounding area differs substantially in *Kranosaura kuttyi* (Figures 2–5) and *Triopticus primus* (Figures 6–9). In *Triopticus primus*, the dorsal opening is larger with an oval cross-section (15.3 mm mediolateral width and 10 mm anteroposterior length). In contrast, the dorsal opening in *Kranosaura kuttyi* is smaller and oval in cross-section, but with a longer anteroposterior axis (4.8 mm mediolateral width and 7 mm anteroposterior length). The edge of the dorsal opening is gently rounded in *Triopticus primus*, whereas the opening in *Kranosaura kuttyi* possesses a weakly developed rim. The depth of the opening is ~15 mm in *Triopticus primus*; this measurement is approximately 68 mm in *Kranosaura kuttyi* (ISIR 268). Both taxa have a depression centered around and surrounding the dorsal opening, but the depression in *Triopticus primus* is wider proportionally, whereas the depression in *Kranosaura kuttyi* is more constrained by parts of the parietal region.

The more lateral portions of the skull tables of *Kranosaura kuttyi* and *Triopticus primus*, the postfrontal-postorbital-squamosal regions, share a few similarities, but this region differs considerably between the two taxa overall. In *Kranosaura kuttyi*, the postfrontal-postorbital-squamosal elements cannot be differentiated, and all of these elements drape over the lateral and dorsal portion of the braincase. In contrast, this part of the skull table of *Triopticus primus* is more differentiated– albeit, these parts may not follow the divisions of the individual skull bones. In *Triopticus primus*, the postfrontal-postorbital part is rounded laterally into a broad knob and is separated from the parietal by a clear cleft. This cleft extends from the dorsal surface ventrally to the supratemporal fenestra. The anterior surface of the postfrontal-postorbital region clearly frames the posterodorsal margin of the orbit, and a lateral rim marks the lateral extension of the orbit. More posteriorly, a posteroventrally-facing supratemporal fenestra is present (6.2 mm anteroposteriorly and 11.8 mm dorsoventrally; Figures 6 and 8), and this opening is likely framed by the parietal, postfrontal-postorbital, and the squamosal. No trace of a supratemporal fenestra is present in *Kranosaura kuttyi*, but this may be the result of breakage. The parietal portion of the skull here forms the posterolateral and posterior portions of the skull. The parietal is a laterally-rounded knob, like that of the postfrontal-postorbital region, and the squamosal appears to lie on the ventral portion of the squamosal region (Figures 6 and 8). The parietal-squamosal region of *Kranosaura kuttyi* extends further ventrally than in *Triopticus primus*; the ventral portion of the parietal-squamosal region of *Kranosaura kuttyi* wraps around and likely would have extended ventrally to much of the braincase (incompletely preserved), whereas in *Triopticus*, this region is clearly dorsal to the occipital condyle.

The more ventral portions of the squamosal are preserved in *Triopticus primus*. It is unclear how much of the posterior knob consists of squamosal, but it is clear that part of the bone ventral to the lateral expansion of the knob must be partially squamosal. A ventral process of the squamosal splits into a medial and a lateral process, and the more medial process articulates with the lateral edge of the paroccipital process. This medial process terminates in a blunt surface ventral to the ventral edge of the paroccipital process. The more lateral process defines the posterior and lateral edges of the squamosal. No clear details of the articulation with the quadrate are observable from external examination or through CT scans.

FIGURE 6 The holotype of *Triopticus primus* (TMM 31100-1030) in (a) dorsal view with interpretive line drawing below, (b) ventral view with interpretive line drawing below, (c) left lateral view with interpretive line drawing below, and (d) posterior view with interpretive line drawing below. ?, unknown; bpt, basipterygoid process; bt, basitubera; cn II, cranial nerve 2 (optic); cp, cultriform process; d, depression; frr, frontal region; l., left; ls, laterosphenoid; mls, midline septum; pal, palatine; par, parietal region; pbs, parabasisphenoid; pit, dorsal pit; por, postorbital/postfrontal region; prb, preorbital boss; pt, pterygoid; oc, occipital condyle; or, orbit; q, quadrate; r., right; sqr, squamosal region; stf, supratemporal fenestra. Arrow indicates anterior direction. Scale bar = 1 cm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The posterior edge of the parietal region continues posterior of the occipital condyle in both taxa. This condition is also clearly present in pachycephalosaurid dinosaurs (e.g., *Stegoceras validum* UALVP 2), and the relative posterior extension of the skull roofs of protopyknosians and pachycephalosaurs is remarkably similar. In *Kranosaura kuttyi* and *Triopticus primus*, a small furrow at the midline originates in the depression surrounding the dorsal opening and trends posteriorly. The furrow terminates before reaching the posterior edge in *Kranosaura kuttyi*, whereas the feature continues to the posterior edge and wraps onto the ventral side of the parietal region to terminate at the posterior level of the occipital condyle in *Triopticus primus*. In dorsal view, the posterior expansion of the parietal region is rounded with a posterior maximum near the midline in *Triopticus primus*, whereas the same margin in *Kranosaura kuttyi* is straight in dorsal view with the maximum posterior extent near the lateral edge. In posterior view, the parietal-squamosal region is mediolaterally narrower in *Kranosaura kuttyi* relative to the more globose equivalent region in *Triopticus primus*. The posterior edge of the skull table is heavily decorated with small rounded knobs in both taxa. In *Triopticus primus*, the knobs are more common and better developed, whereas the deep foramina are more common near the midline in *Kranosaura kuttyi*. The parietal region roofs a deep posteriorly-opening fossa between the ventral surface of the parietal region and the supraoccipital of the braincase in *Triopticus*; this region is not well-preserved in *Kranosaura kuttyi*.

Quadrate – Only the dorsal portion of the left quadrate is preserved in *Triopticus primus* (Figures 6 and 8), and much of that quadrate is obscured by the surrounding elements. The head of the quadrate is hidden by the squamosal and the paroccipital process in posterior view and by the squamosal laterally. The posterior edge of the quadrate is mediolaterally narrow, and part of the pterygoid process remains in articulation with the pterygoid. The angle of the posterior margin of the shaft appears to be positioned anteroventrally; this suggests that the orientation of the quadrate in at least *Triopticus primus* was similar to the heavily anteroventrally-angled quadrates of pachycephalosaurid dinosaurs (e.g., *Stegoceras validum* UALVP 2).

Braincase – The braincase mostly is preserved in *Triopticus*, whereas the braincase of *Kranosaura kuttyi* is missing in ISIR 269 because the region has been over-prepared and details have either been removed or eroded. In ISIR 268, a portion of the top of the braincase is preserved (Figure 3b,c).

The braincase of *Triopticus primus* consists of nearly all portions preserved at least from either the left or right sides. A complete endocast was illustrated, described in detail, and put in comparative context by Stocker et al. (2016). The right side of the braincase was damaged prior to excavation; the lateral portion of the otooccipital (=paroccipital process) and many of the lateral extremes of the braincase elements are damaged. Additionally, a large crack that transects the entire skull (Figures 6, 8 and 9) cuts through the braincase from the lateral portion of the right prootic through the anterior portion of the parabasisphenoid on the left. The anterior half of the cultriform process is offset laterally.

The occipital condyle of *Triopticus primus* lacks a notochordal pit, and the exoccipitals are firmly attached without any visible suture between the elements. Ventrally, the occipital condyle has a short neck without much differentiation between the rounded portion of the condyle and the rest of the basioccipital. On the ventral surface of the basioccipital, a distinct projection tapers ventrally at the midline (Figures 6 and 8). The process is mediolaterally compressed and is more expanded posteriorly than anteriorly. This process appears unique among archosauriforms. Anterior to the ventral process, a pit is present that is separated from the parabasisphenoid depression by a bridge of bone (Figures 6 and 8). Although the suture between the basioccipital and parabasisphenoid is not apparent, the anterolateral side of the basioccipital possesses the posterior portions of the basitubera.

The left otooccipital of *Triopticus primus* is complete, but the right is missing the lateral extremes. In posterior view, the exoccipital portion of the otoocciptial extends around and forms the circular foramen magnum; it is not clear if the exoccipitals meet at the midline dorsal to the foramen magnum or if the supraoccipital forms part of the edge of the foramen magnum. The dorsolateral edges of the foramen magnum are deflected posteriorly so that posteriorly directed tabs of bone roof the opening. This morphology results in a small shelf that likely fit the proatlas or the atlas vertebra.

More ventrally, the medial portions of the exoccipitals appear to meet on the midline to form the ventral edge of the foramen magnum, unlike in dinosaurs where there is a clear gap (Nesbitt, 2011). The lateral sides of the exoccipitals bear two foramina that are aligned in a near-horizonal plane. The more posterior opening is larger, and both sit in a shallow fossa. The openings are interpreted as the exits for cranial nerve XII given their similar positions and pathway compared to other archosauriforms (Gower, 2002; Gower & Sennikov, 1996; Gower & Walker, 2002; Sobral et al., 2016). The exits for cranial nerve XII are separated from the metotic foramen by a laterally expanded lamina. The lateral extent of the lamina fails to completely obscure the metotic foramen in posterior view and the lamina parallels the ventral ramus of the opisthotic.

The ventral ramus of the opisthotic of *Triopticus primus*, which divides the metotic foramen from the fenestra ovalis, originates on the ventral edge of the paroccipital process (Figure 8). The edge trends ventromedially and slightly anterior to terminate on the lateral portion of the posterior extent of the basioccipital portion of the basitubera. Moreover, the ventral end of the ventral ramus of the opisthotic slightly expands into a pendant shape than that observed in other archosauriforms (Gower & Sennikov, 1996). The lateral extent of the ventral ramus of the opisthotic is far beyond the more posterior lamina of the middle of the braincase so that the ventral ramus of the opisthotic is easily observable in posterior view. This is similar to that of stem archosaurs (Gower & Sennikov, 1996) and pseudosuchians (Gower & Nesbitt, 2006) rather than what is observed in dinosaurs and their close relatives (Nesbitt, 2011).

A circular fenestra ovalis of *Triopticus primus* lies in a fossa anterior of the ventral ramus of the opisthotic. The fossa is restricted

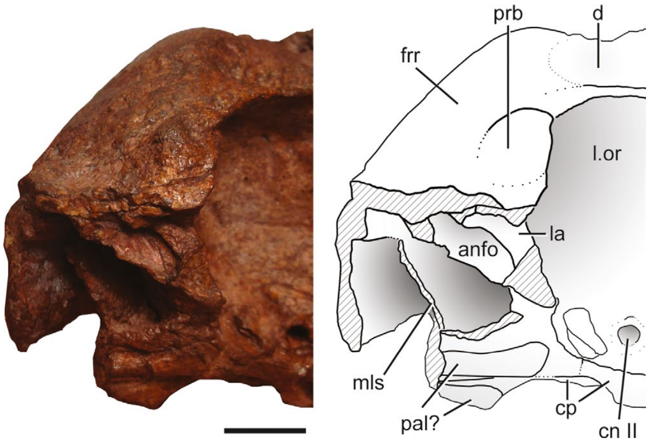


FIGURE 7 The holotype of *Triopticus primus* (TMM 31100-1030) in anterolateral view with interpretive line drawing. ?, unknown; anfo, antorbital fossa; cn II, cranial nerve 2 (optic); cp, cultriform process; d, depression; frr, frontal region; l., left; mls, midline septum; la, lacrimal; pal, palatine; prb, preorbital boss. Broken surfaces indicated by cross hatching. Scale bar = 1 cm

medially near the fenestra ovalis and continues laterally between the ventral ramus of the opisthotic and the posterior portion of the prootic; this surface is concave ventrally and terminates well short of the posterolateral termination of the paroccipital process.

The dorsal portion of the otooccipitals of *Triopticus primus* is deflected posterodorsally and is nearly flat and smooth. Laterally, the otooccipitals slightly expand dorsally and ventrally to form an anteroposteriorly-compressed paroccipital process. The lateral extent of the paroccipital process is nearly straight, and this part meets a distinct process of the squamosal. Ventrally, the paroccipital is thickened anteroposteriorly relative to the medial portion that bears the ventral ramus of the opisthotic. Dorsally, the dorsal edge of the otooccipital is concave and forms the ventral border of an oval (mediolateral maximum length 9.2 mm by dorsoventral maximum length 3.2 mm) posttemporal fenestra.

The otooccipital of *Triopticus primus* meets the supraoccipital in a posterodorsally-open fossa located at the dorsal portion of the elements. The midline of the supraoccipital possesses a rounded ridge typical of archosauriforms (Gower & Sennikov, 1996), but not a sharp ridge or pillar as in rhynchosaurs (Dilkes, 1998).

Much of the prootic is covered by the pterygoid anterolaterally in the left side and is shattered on the right side. Ventrally, the posterolateral edge of the prootic splits just anterior to the fenestra ovalis. Within this split, a small foramen marks the exit for cranial nerve VII based on similar positions in other archosauriforms (Gower, 2002; Gower & Sennikov, 1996; Gower & Walker, 2002; Sobral et al., 2016). The more anterior side of the split ridges expands ventrally into a pendant. The broken right side reveals the location for the exit of cranial nerve V at the border of the prootic and the laterosphenoid. The opening is tear-drop shaped with the tapered portion directed anteriorly; most of the border of the exit of cranial nerve V is formed by the prootic, whereas it appears the laterosphenoid forms only just a small portion of the anteriormost edge of the opening. More ventrally, the anterior process of the prootic tapers far anterior of the opening (Figures 6 and 8).

The parabasisphenoid of *Triopticus primus* is largely oriented horizontally (i.e., the ventral surface is nearly in the same horizontal plane anteriorly to posteriorly) as in early-diverging archosauriforms (e.g., *Proterosuchus*; Clark et al., 1993; Gower & Sennikov, 1996; Ezcurra, 2016) rather than the more verticalized (anterior portion much more ventrally rotated) braincases of crown archosaurs (Gower, 2002; Gower & Sennikov, 1996). Much of the basitubera seem to be formed by the posterior portion of the parabasisphenoid. Together with the basioccipital component of the basitubera, the basitubera (anteroposterior length = 4.8 mm) are crescent shaped in ventral view with a distinct rim laterally and a depression medially. The anterior portion of the basitubera terminates well lateral to the midline, but a rounded ridge connects the basitubera across the midline. Anterior of this ridge, a clear anteroposteriorly-elongated depression is present on the midline between the basitubera and the basipterygoid processes. No clear foramina for the internal carotids are present on the ventral surface (as in most non-archosaurian archosauriforms and some crown archosaurs; Nesbitt, 2011), but a crack transecting the ventral surface may be obscuring these openings. The ventral tips of the basipterygoid processes are both broken, but it appears that the lateral extent of the basitubera and the basipterygoid processes are nearly equal. Anteriorly, the parabasisphenoid transforms into a long cultriform process. This process is artificially compressed onto the midline between the orbits. The height and anteriormost portion of the cultriform process cannot be determined.

The lateral sides of the parabasisphenoid are largely obscured by the pterygoid, but the broken surface of the right side shows that there was a lateral depression roofed by a ventrolaterally-extending lamina of bone. It is not clear if the internal carotids entered the braincase laterally in this depression as they do in some crown archosaurs (e.g., dinosaurs, aetosaurs, loricatans).

The laterosphenoids of *Triopticus primus* are well-preserved and easily seen within the orbits. This ossification contacts the prootic posteriorly, the ventral lamina of the frontals dorsally, and stretches anteriorly to transect the orbit; the anterior termination is obscured by crushing and other elements. The dorsal edge is fused to the frontal, and this contact is likely marked by an anteroposteriorly-oriented groove that originates posteriorly in a foramen (Figures 6 and 8). The identification of this foramen is difficult because of the aberrant morphology of *Triopticus primus*, but its position dorsal and anterior to the cotylar crest suggests this foramen may correspond to the ophthalmic artery foramen of other archosaurs and their kin (Clark et al., 1993; Small, 2002). Another parallel groove also leads to a small foramen; this foramen is near, but anterior to, the ventral portion of the cotylar crest. We identify this foramen as the exit for cranial nerve III or IV based on similar positions in other archosaurs and kin (Clark et al., 1993; Small, 2002). The largest foramen is symmetrically located at the ventral edge of the laterosphenoids (Figures 6 and 8). We interpret this large foramen as the exit of cranial nerve II based on a similar position in other archosaurs and their close relatives (Clark et al., 1993; Small, 2002).

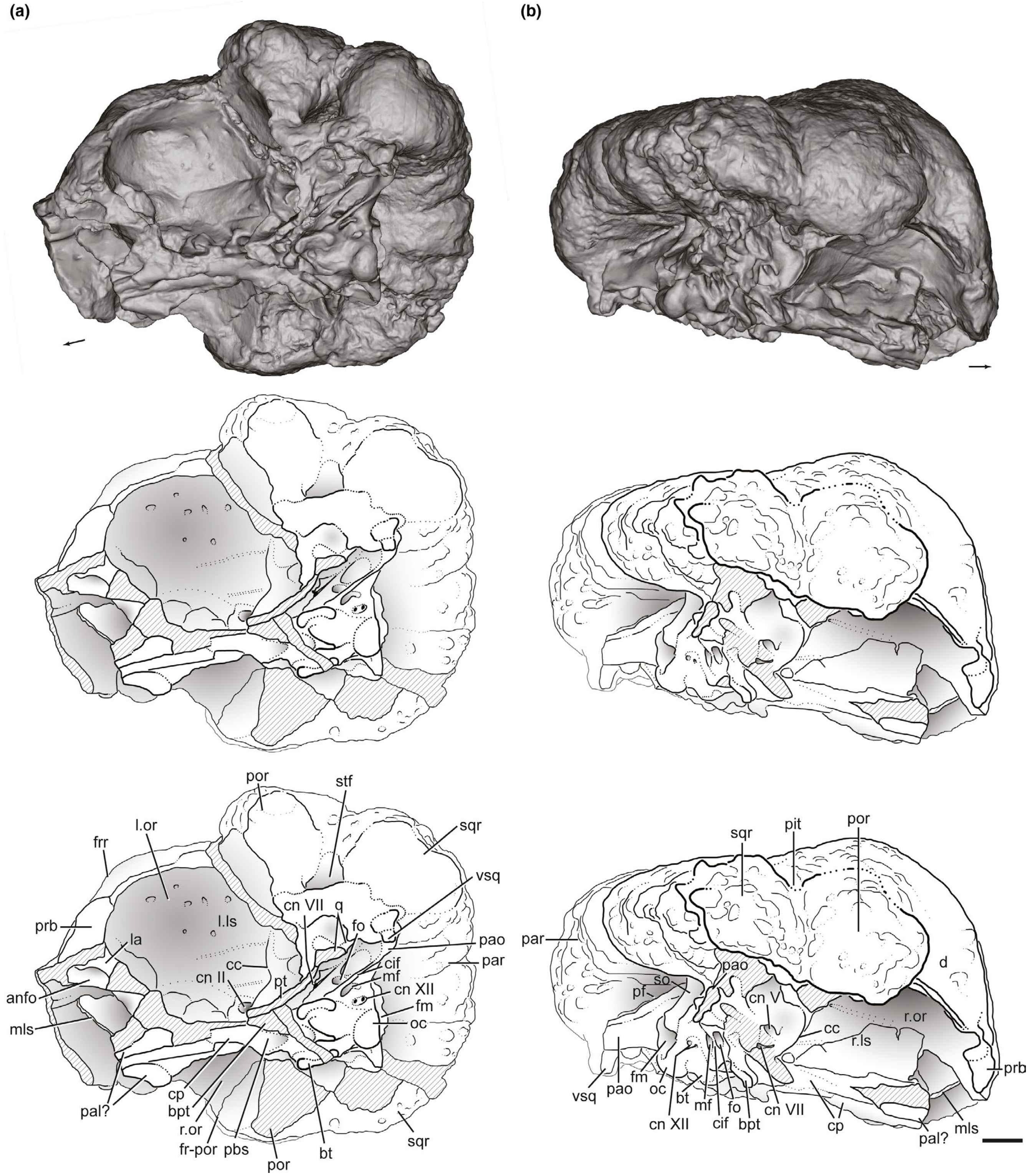


FIGURE 8 The holotype of *Triopticus primus* (TMM 31100-1030) in (a) ventrolateral view as a digital model (top), detailed line drawing (middle), and labeled line drawing (bottom) and in (b) right lateral view as a digital model (top), detailed line drawing (middle), and labeled line drawing (bottom). ?, unknown, anfo, antorbital fossa; bpt, basipterygoid process; bt, basitubera; cc, cotylar crest; cif, crista interfenestralis; cn II, cranial nerve 2 (optic); cn V, cranial nerve 5 (trigeminal); cn VII, cranial nerve 7 (facial); cn XII, cranial nerve 12 (hypoglossal); cp, cultriform process; d, depression; fm, foramen magnum; fo, fenestra ovalis; fr-por, frontal-postorbital/postfrontal region suture; frr, frontal region; l., left; la, lacrimal; ls, laterosphenoid; mf, metotic foramen; mls, midline septum; pal, palatine; par, parietal region; pao, paroccipital process of the opisthotic; pbs, parabasisphenoid; pf, posttemporal fenestra; pit, dorsal pit; por, postorbital/postfrontal region; prb, preorbital boss; pt, pterygoid; oc, occipital condyle; or, orbit; q, quadrate; r., right; sqr, squamosal region; stf, supratemporal fenestra; vsq, ventral process of the squamosal. Broken surfaces indicated by cross hatching. Arrow indicates anterior direction. Scale bar = 1 cm

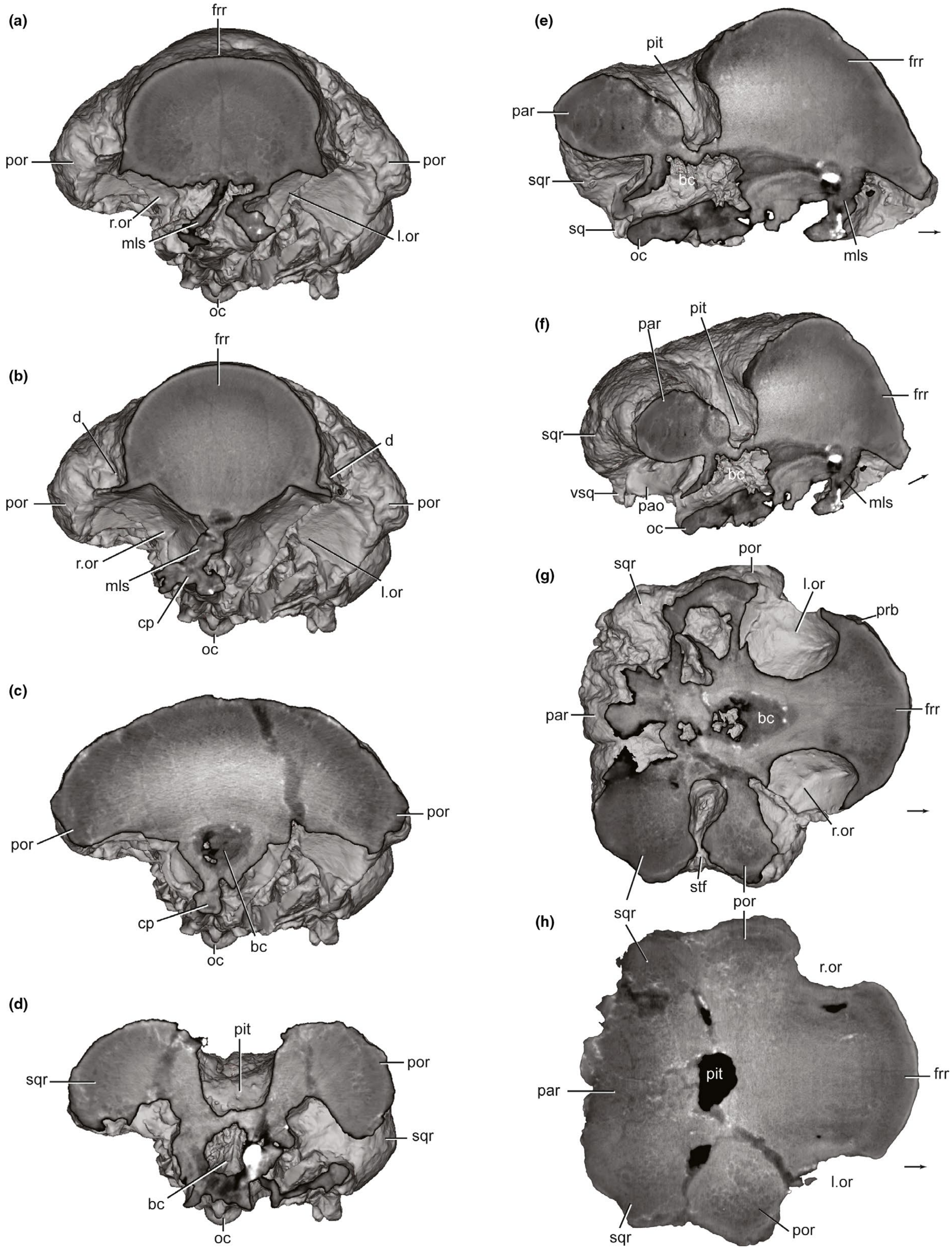


FIGURE 9 Digital reconstructions of the holotype of *Triopticus primus* (TMM 31100-1030) to show cross sections throughout the skull. Coronal sections through the skull (a–d) starting anteriorly (a) and proceeding posteriorly to (d). Sagittal section through the skull (e) in right lateral view and a skewed posterolateral (f) view. Transverse section through the skull just ventral to the top of the orbits (g) and a reconstructed image (h) through the 'dome' just dorsal to the orbits. bc, braincase; cp, cultriform process; d, depression; frr, frontal region; l., left; mls, midline septum; par, parietal region; pao, paroccipital process of the opisthotic; pit, dorsal pit; por, postorbital/postfrontal region; oc, occipital condyle; or, orbit; r., right; sqr, squamosal region; stf, supratemporal fenestra; vsq, ventral process of the squamosal. Arrows indicate anterior direction

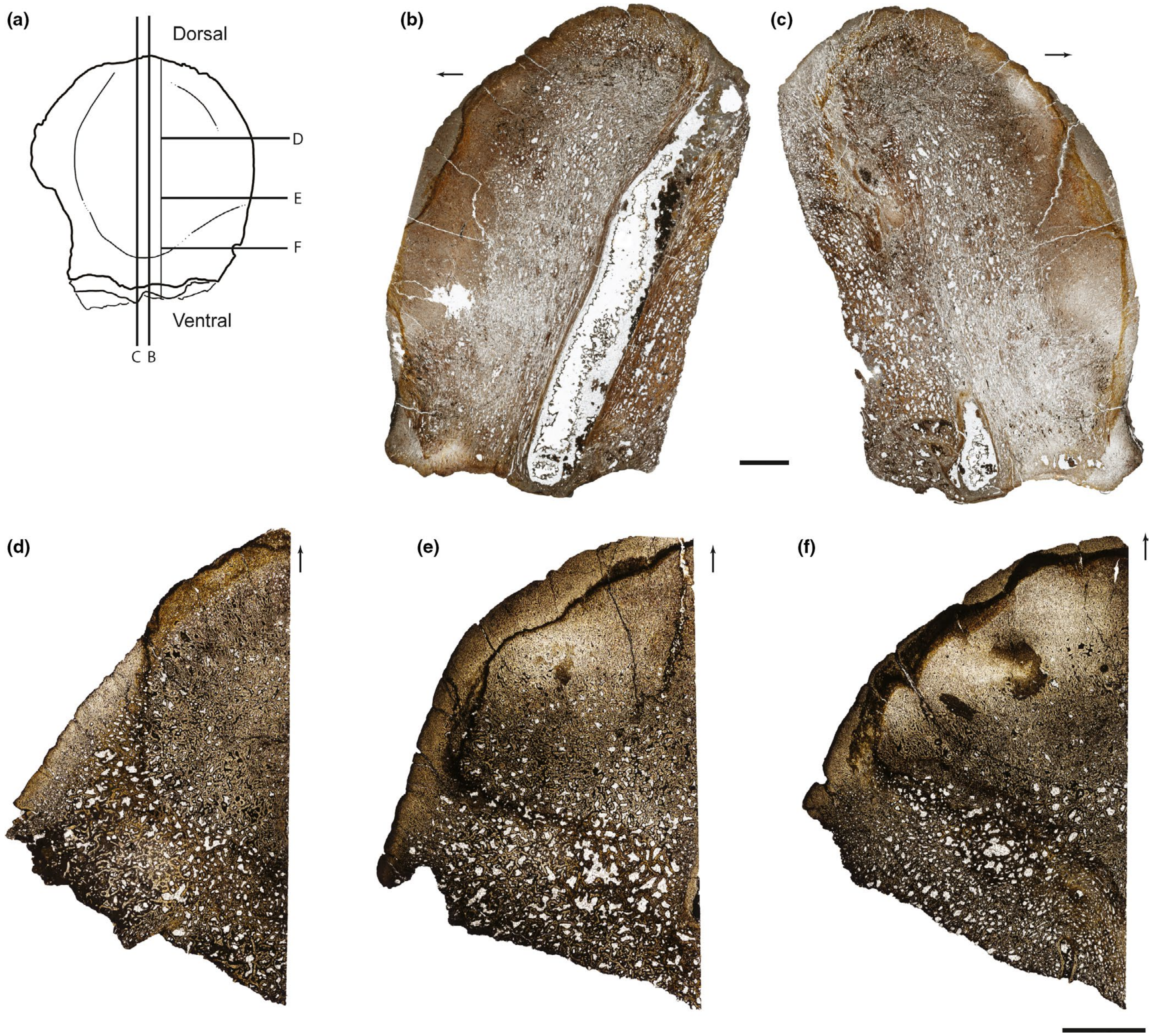
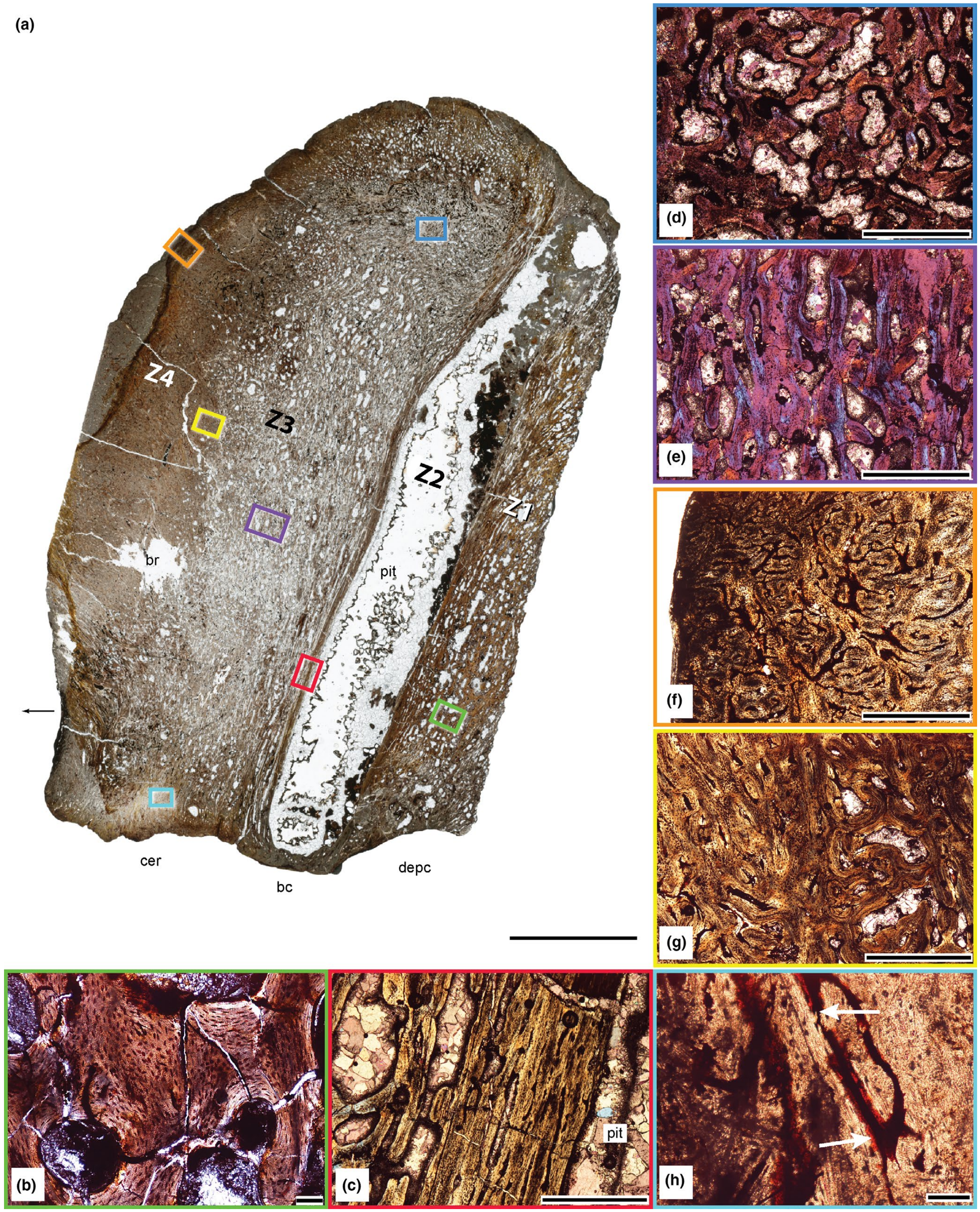


FIGURE 10 Histological sections of *Kranosaura kuttyi* (ISIR 268). (a) Index key of where the thin sections were taken on ISIR 268. (b) Midline sagittal section (ISIR 268. FrPa1-L1). (c) Mirror image of sagittal section just lateral to the midline (ISIR 268. FrPa1-L2). (d) Dorsal, left lateral half of specimen (ISIR 268. FrPa1-1). (e) Middle, left lateral half of specimen (ISIR 268. FrPa1-2). (f) Ventral, left lateral half of specimen (ISIR 268. FrPa1-3). Black arrows indicate anterior direction. Scales bars = 1 cm

A vertical, laterally expanded, and sharp crest lies in the posterior one-third of the laterosphenoid. We interpret this crest as the cotylar crest, and the size of this crest is proportionally larger than those of any other archosauriforms currently available for study. A shallow fossa lies dorsal and posterior to the crest where it contacts the skull roof. Just ventral to this, a posteroventrally-oriented pillar

FIGURE 11 Histology of *Kranosaura kuttyi* (ISIR 268) at the midline, sagittal section. (a) Full sagittal section showing the locations of magnified histology images by color, and the 4 zones designated Z1-Z4. (b) (Green) Woven trabecular spicule with minimal lamellar veneering on vascular canal walls. (c) (red)) Compact, radial fibrolamellar wall of the median pit. (d) (blue) Woven, isotropic, trabecular cancellous tissue lacking lamellar veneering. Photographed with a lambda compensator and revealing no birefringence. (e) (purple) Radially oriented fibolamellar tissues of Zone 3. Photographed with a lambda compensator showing bifringence of lamellar tissues veneering trabeculae. (f) (orange) Compact fibrolamellar bone in Zone 4 with a reticular type tissue patterning. (g) (yellow) Transition tissues between Zone 3 and Zone 4. Note the fibrous trabeculae are further separated in Zone 3 than in Zone 4, and that the trabeculae of Zone 4 are close enough to allow osteonal development within the vascular spaces. (h) (aqua) A vascular canal containing iron that has a black opaque color when thick and a translucent red color (white arrows) where it is thinned. This iron infilling obscures the walls of many vascular canals making it difficult to impossible to determine whether there has been any osteoclastic resorption. Scales = 1 cm in a, 1 mm in c-g, and 100 μm in b, h



of bone delimits the laterosphenoid contribution to the exit of cranial nerve V.

The referred specimen of *Kranosaura kuttyi* (ISIR 268) preserves the dorsal impression of the endocast on the ventral surface of the preserved portion (Figure 3b,c). The midline endocast is separated into three regions. The anteriormost region (1) expands dorsally at the midline; (2) lies between the posterior portion of the orbits; and (3) expands more laterally than the other two regions. Based on its position, broad dorsal expansion, and comparisons to *Triopticus primus* (Stocker et al., 2016), we interpret this part of the endocast impression as pertaining to the cerebrum. More posteriorly, the endocast impression is restricted by the ventrally expanded portion of braincase (Figures 3 and 10), thus dividing the anterior and posterior portions of the endocast impression. As revealed through CT data and the histological sections, the middle portion of the endocast impression has a thin lamina of bone separating the endocast cavity from the dorsal opening that extends through the dome. As a result, the dorsal pit is not connected to the endocast. Similarly, the dorsal opening of *Triopticus primus* is separated from the endocast in the homologous region (Stocker et al., 2016; Figure 2a). The posterior third of the endocast impression expands dorsally and becomes more laterally restricted posteriorly. We interpret this portion of the endocast impression as the dural peak that is common to *Triopticus primus* (Stocker et al., 2016; Figure 2a–c) and plesiomorphic for archosauromorphs (Holloway et al., 2013; Sampson & Witmer, 2007). A dural peak is absent in pachycephalosaurid dinosaurs (Stocker et al., 2016). Two grooves that flank the posterior portion of the endocast (Figure 3) are interpreted as the ventral surface of the parietals.

Within the Orbit – The orbit of *Triopticus primus* is circular in lateral view, and the left and right orbits are separated by a combination of large laterosphenoids and likely part of a ventral process of the frontal; however, the identification of this ventrally extended lamina of bone is not clear. This may be part of an orbitosphenoid, but we cannot determine how many elements this midline structure comprises. Furthermore, it is not clear if these frontal laminae converge anteriorly to form a single lamina that is visible in anterior view stretching from the ventral surface of the skull roof to the palatal elements (Figures 6 and 8).

The interorbital surface is concave laterally and ventrally, and the surface is largely smooth with a number of small foramina in an anteroposteriorly-oriented groove (Figures 6 and 8). An anteroposteriorly oriented series of foramina are located on the frontal portion interorbital surface near an inflection point marking the junction between the dorsoventrally-thin roof of the orbit and the more medial portion of the frontal. The anteriormost foramen is the largest and deepest, whereas they get smaller and shallower posteriorly. A few other foramina are present ventral to the larger foramina. More ventrally, an anteroposteriorly-oriented groove (Figure 8) appears to mark the contact between the frontal and the laterosphenoid.

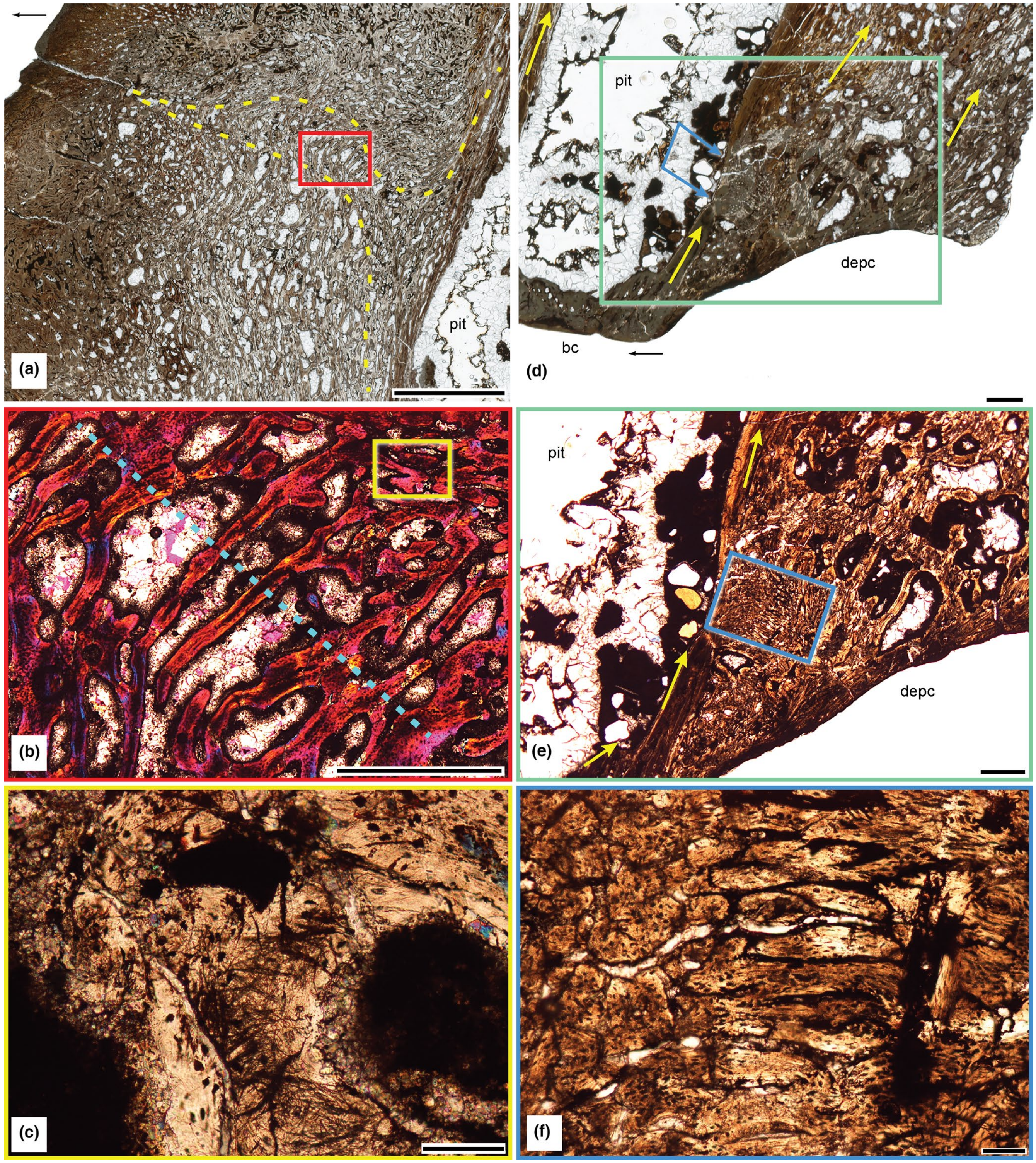
The posterodorsal portion of the orbit is formed by the postfrontal-postorbital knob, and a clear rim separates the external surface of the skull from the smooth interior portion of the orbit. The only clear suture in the entire skull of *Triopticus primus* lies between the postfrontal-postorbital knob and the frontal. This suture coincides with a large crack in the left side (Figures 6 and 8) but is clearly visible as a slight step on the right side (Figure 6). The suture originates medially at the dorsal end of the cotylar crest of the laterosphenoid and trends dorsolaterally to terminate at the anterior extent of the postfrontal-postorbital knob and the posterior termination of the dorsoventrally-thin roof of the orbit of the frontal region. The suture is not interdigitated. The anterior portion of the orbit of *Triopticus primus* is largely obscured by distorted portions of the palate and the braincase.

The orbital region of *Kranosaura kuttyi* is not preserved in ISIR 269, whereas only a small portion of the orbital region is preserved in ISIR 268 (Figure 3). A small surface represents the ventral portion of the postorbital/postfrontal bone and the posterodorsal border of the orbit. The surface bears small foramina that open into a groove posteromedially. The cerebrum portion of the endocast lies medial to this orbit border.

Palate– The palate of Protopyknosia is poorly known other than the fragmentary remains present in the holotype of *Triopticus* (TMM 31100-1030). Portions of the left pterygoid remain in articulation with the pterygoid ramus of the quadrate (see above) and the basipterygoid process of the parabasisphenoid, but none of the pterygoid is preserved ventral to the basitubera of the braincase. The pterygoid curves posterolaterally from the basipterygoid process of the parabasisphenoid to meet the pterygoid wing of the quadrate. The distance between these two articulation sites is relatively short given the medial shift of the quadrate in *Triopticus* compared to that of other reptiles.

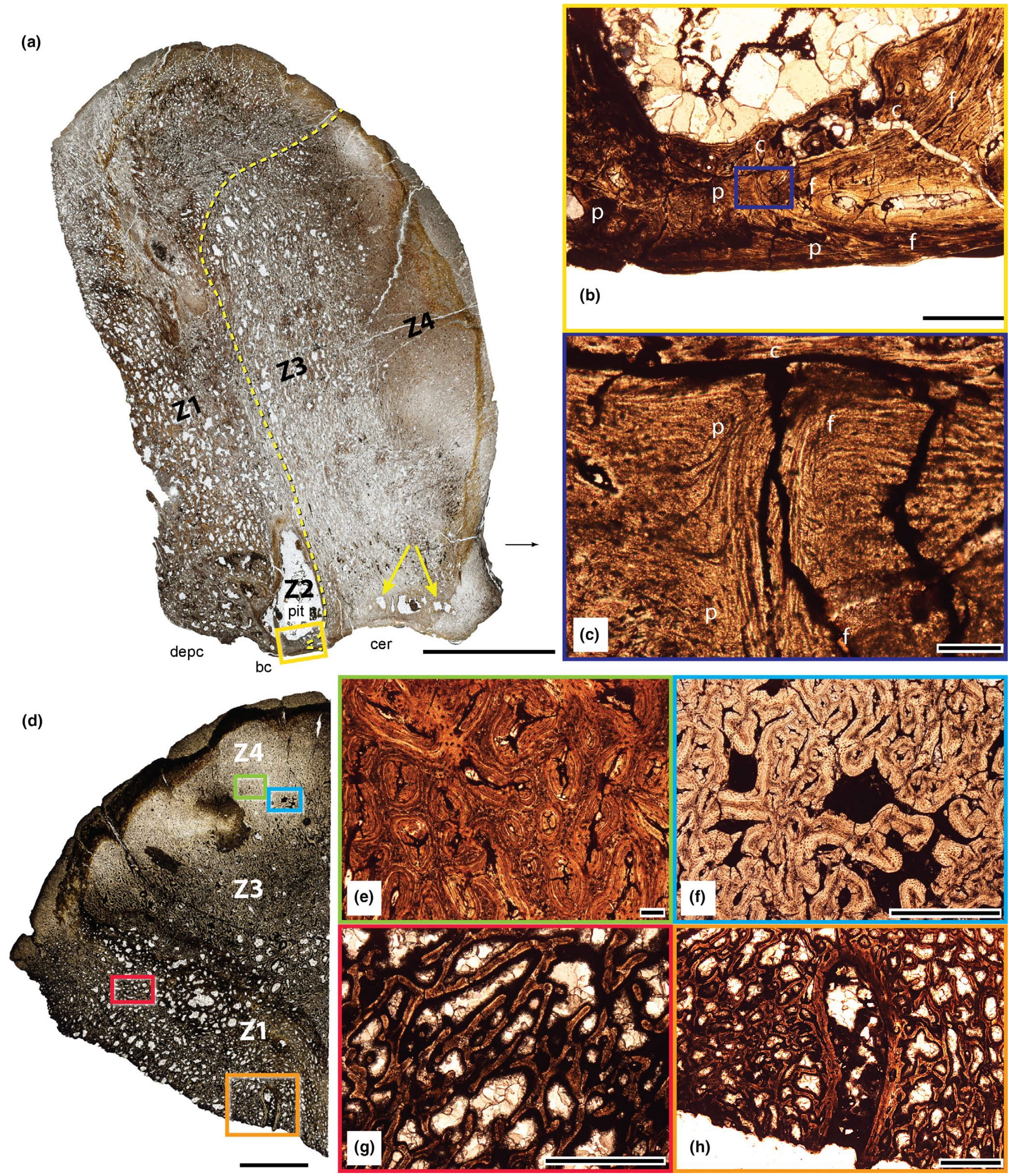
Two small pieces of bone symmetrically distributed across the midline in the anterior portion of the preserved skull of *Triopticus primus* are interpreted as parts of the palatines. The posteriormost

FIGURE 12 Histology of *Kranosaura kuttyi* (ISIR 268) at the midline, sagittal section. (a) Antero-dorsal region revealing the path (yellow dashed lines) of what appears to be a possible, nearly obliterated suture. Note the much coarser cancellous tissue ventral to the proposed suture and much finer cancellous tissue dorsally. The dorsal tissues contain abundant non-oriented fibers, whereas the tissues ventrally lack fibers. The red box shows the location of b. (b) (red) Cancellous trabeculae that unite the dorsal, fine cancellous region to the ventral coarse cancellous region. The dotted light blue line is oriented perpendicular to the "suture," and approximates the junction point of the two sides. The yellow box is the position of c. (c) (yellow) Image showing the fibrous, cancellous tissue containing abundant disoriented fibers and osteoclast widened erosion rooms. (d) Posteroventral region of the mid-line sagittal section showing the general orientation of the radial tissues (yellow arrows), and the location of what appears to be a break in the fibrolamellar wall of the dorsal pit (blue arrows). The turquoise box indicates the position of e. (e) (turquoise) Photo showing unusual and oddly oriented tissues and the general orientation of the radial tissues (yellow arrows) in the region between the dorsal pit and the dorsal surface of dural peak of the brain endocast. Large erosion rooms dorsally, and smaller erosion rooms ventrally. The blue box shows the position of f. (f) (blue) Fibrolamellar, tissue, longitudinally oriented to the left (anteriorly) and right (posteriorly) with a short section of circumferential vascularity in between. All of these tissues appear very immature compared to the surrounding tissues. bc, dorsal surface of the endocast that caps the dorsal pit; dpec, dorsal surface of dural peak of the brain endocast; pit, dorsal pit. Scales = 1 cm in a, d, 1 mm in b, e, and 100 µm in c, f. Black arrow indicates anterior direction



portion of these bones taper posteriorly, but contact between the palatines and the pterygoids is not preserved. The anterior and lateral portions of the palatines are not preserved either.

Lacrimal – A dorsal portion of the left lacrimal is present in *Triopticus primus* (Figure 7). The fragment is slightly displaced dorsomedially so that the dorsal portion of the lacrimal is hidden by the lateral portion of the prefrontal boss. The ventral one-half to two-thirds of the lacrimal is missing. The lateral surface of the preserved portion indicates that *Triopticus primus* possessed an antorbital fossa and, more anteriorly, an antorbital fenestra. The posterodorsal corner of the antorbital fossa is covered laterally by a thin lamina. The anterior edge of the lacrimal is mediolaterally thin and outlines the posterodorsal part of the antorbital fenestra.



2.5 | Histology interpretation and comparisons

Five thin sections were cut from the referred specimen of *Kranosaura kuttyi* (ISIR 268), two sagittally, one of which was centered, and the other adjacent, right lateral, and three transverse from the left lateral half, in sequential thirds (see Figure 10). The osteohistologic preservation is relatively good with some regions of the thin sections affected by various diagenetic alteration described in more detail below. Overall, the dome-like structure is composed almost exclusively of woven, cancellous tissues (Figures 10–12) forming trabeculae with varying degrees of primary, osteonal, and lamellar infilling. The mid-line sagittal section (Figure 11a)

FIGURE 13 Histology of *Kranosaura kuttyi* (ISIR 268). (a) Sagittal section, right-lateral from the mid-line showing the lateral end of the dorsal pit and some moderate sized sinus like cavities (yellow arrows) located over the medial portion of the right orbit at the midline. p = parietal, f = frontal, c = capping. (b) The bone barrier at the ventral end of the median pit shows what we hypothesize to be the sutural junction of the parietal and frontal in calvarial tissues above the braincase. The letter 'p' shows the extent of the anterior process of the parietal bone where it underlies the posterior end of the frontal. The 'f' shows the frontal bone as it laps onto the parietal. The bone designated 'c' appears to be a capping tissue over the suture and likely originated from either a branch of the frontal or parietal or both. (c) is a magnified image of B showing the orientation of the collagen fibers at the suture. Note that these fibers curve at 90° angles upon reaching the suture. Numerous Sharpey's fibers are visible on both sides of the suture. (d) Transverse section cut left lateral from the midline (FrPa1-1) showing the tissue zones and locations of the magnified images e-h(pink). (e) (pink) Mature primary osteons found in the compact anterior side of ISIR 268 reveal a more organized looking tissue in transverse section compared to the same area in the longitudinal section. (f) (blue) image showing the transition area between Zone 3 and Zone 4. Note as seen in Figure 11g that the trabeculae of Zone 3 are further separated creating larger vascular cavities. (g) (red) The trabeculae in the coarse cancellous Zone 1 are further apart than in Zone 3, and the islands of fibrous tissue is minimal. (h) (orange) A small vacuity lined with fibrolamellar tissue surrounded by cancellous tissue. This vacuity is on the broken posterior side of the specimen, and may or may not have connected to the median pit. Scales are 1 cm in a–b, 1 mm in c, and 100 µm in d. Black arrow indicates anterior direction

reveals the generalized salient features of the dome, visually divisible into four zones.

Each zone is oriented slightly askew from vertical and described from posterior to anterior: Zone 1, the posteriormost Zone, lies posterior to the median pit and is composed of coarse, cancellous, and woven trabeculae with intervening vascular spaces that are primarily oriented radially. None of the trabeculae reveal evidence of osteoclastic resorption, as evidenced by a lack of Howship's lacunae. Primary osteonal lamellar veneering of the trabecular walls is minimal (Figure 11b). Zone 2, anterior from Zone 1, is defined by the "median pit," a centrally located vacuity that extends dorsoventrally from a thin bony barrier above the braincase and exits on the broken dorsoventral surface of the specimen. The median pit is bound by compact, fibrolamellar radial tissue that averages 0.5 mm in thickness (Figure 11c). The bone barrier at the ventral end of the median pit directly over the braincase is composed primarily of fibrolamellar tissues with complex orientations and a few rare secondary osteons (described in detail below). Zone 3 lies anterior to the median pit, is cancellous and generally less coarse than the tissues found in Zone 1. Most of the trabeculae in the region of Zone 3 are oriented radially (Figure 11e), except in its dorsal cap present in the dorsal 1/3 of the specimen (Figure 11d). The trabeculae of the dorsal cap (Figure 11d) are not only unorganized, but are also isotropic under crossed nicols. The amount of osteonal lamellar infilling in Zone 3 is variable by location. In the dorsal cap region, the woven trabecular tissues are virtually devoid of lamellar veneering (Figure 11d) whereas the woven trabecular tissues more centrally located in Zone 3 (Figure 11e) are nearly all veneered with primary lamellar tissues. Zone 4 is characterized by a dense appearance, afforded by both a greater volume of woven bone, and more mature osteonal development (Figure 11f). Where the tissues of Zone 3 transition to Zone 4 the differences in osteonal development are apparent (Figure 11g). Here, the large open spaces are not erosion rooms formed by osteoclast actions but represent larger space between bony trabeculae. In some vascular spaces of Zones 1, 3, and 4, the walls of the caverns appear scalloped by osteoclasts, but upon close examination, diagenetic minerals appear to be responsible for these features. Iron, most often seen as a black or red infilling of the vascular space, appears to have invaded the vascular walls, obscuring much of the original surfaces (see Figure 11h). There is also evidence of alteration of the vascular walls by crystal growth within the cavities.

Two anomalous areas present in the midline sagittal section of ISIR 268 warrant further description and interpretation here. The first is an unusual tissue that traverses across the area anterior to the dorsal pit about two-thirds of the distance from the ventral surface to the dorsal surface (Figure 12a). The structure highlighted by the yellow dashed line confirms its subtle wedge-like appearance. This distinctive wedge-like structure is very similar to the nearly obliterated suture (see magnified view in Figure 12b) described by Kulik and Sidor (2019: Figure 3d). Nearly obliterated sutures often have morphologies that look similar to a zipper with a zig-zag appearance (see Bailleul & Horner, 2016). This zig-zag appearance is produced by fingers or processes originating from the two respective elements that are to be joined, fitting more snugly in between one another as the union progresses. The end result is a tight union with the suture obliterated. We hypothesize the suture to trend perpendicular to the joined bony fingers shown by the blue dashed line in Figure 12b. The trabecular processes of the suture contain varying numbers of extrinsic fibers that are most likely Sharpey's fibers (Figure 12c).

The second anomalous area in ISIR 268 is located in the posteroventral area of the midline sagittal section (Figure 12d). As noted previously, the median pit is bordered by a 0.5 mm thick, radially oriented, fibrolamellar tissue. Interestingly, this border is consistent in thickness except for a short section in the posteroventral location pointed out by the two blue arrows in Figure 12d. Here, this 2 mm portion of the border wall with its radially oriented tissues is disrupted and the vascular canals in the immediate area take on a "circumferential" orientation, perpendicular to all of the radially oriented tissues surrounding this region (Figure 12e,f). All of these disoriented tissues are highly vascularized, fibrolamellar (Figure 12f), and bordered by the large vascular spaces of the coarse cancellous tissues of Zone 1 (Figure 12e).

The right lateral sagittal thin-section (Figures 10c and 13a) exposes the basal portion of the median pit which is slightly expanded at its ventral end as confirmed by CT scans. With the median pit (Zone 2) absent in the more dorsal areas of this section, the interface between Zone 1 and Zone 3 appears as a slight difference in the coarseness of the cancellous tissues (Figure 13a). This section also reveals a series of sinus cavities (Figure 13a, yellow arrows) located lateral to the midline and probably over the medial side of the orbit. The borders of these cavities are lined with endosteal-like tissues. The yellow line in Figure 13a is where we hypothesize a suture to exist. The dorsal portion of this line tracks the zipper-like structures described earlier (Figure 12a,b) and the ventral end of the yellow line terminates in the tissue barrier between the median pit and roof of the braincase. Here we see what appears to be a wedge-shaped suture between the frontal and parietal bones of the calvarium (Figure 13a–c). The suture is nearly obliterated and the tissues in this region are not well-preserved, but collagen fiber orientations (Figure 13c) suggest a union of two and perhaps three different ossification centers designated by the letters ‘f’ (frontal), ‘p’ (parietal), and ‘c’ (capping) (Figure 13b,c). Radially oriented fibrolamellar tissues present in the anterior wall of the median pit originate in the mid-portion of the barrier as a V-shaped wedge, designated by the letter ‘f’, and sandwiched between tissues designated by the letters ‘p’ and ‘c’. These wedge-shaped tissues wrap around the anterior portion of the median pit. The ‘p’ (parietal) tissues originate in the barrier abutting and underlying the wedge-shaped structure of ‘f’ (frontal) tissues, and wrap posteriorly around the median pit. The ‘c’ (capping) tissues appear to be extraneous tissues that overly this suture. These ‘c’ tissues likely originate from both anterior (the frontal) and posterior (the parietal, as well as lateral directions (frontal and/or parietal).

The sequential transverse sections (Figure 10d–f) reveal that at least a thin veneer of the dense Zone 4 tissues (see Figure 11a) wrap around the sides of the dome. This is best observed in Figure 10e,f. The dorsal-most section (Figure 13d–h) is the best preserved of the three sections and reveals the extent of lamellar infilling in the multiple Zones. The dense tissues of Zone 4 reveal a disorganized reticular-like pattern in the sagittal section (Figure 11f) and are much more organized in transverse view (Figure 13e), revealing mature, longitudinal osteons. Adjacent to these mature osteons are intervening islands of fibrous trabeculae. In the transitional area between Zone 4 and Zone 3, the trabeculae are spaced further apart, resulting in larger intervening cavities (Figure 13f). In Zone 1, the trabeculae are so far apart that osteons are unable to form and the primary lamellar tissues are deposited as veneers on the trabecular spicules (see Figure 13g,h). A small vacuity enters the coarse tissues of cancellous Zone 1 along the broken edge of ISIR 268 (Figure 13h). This vacuity is lined with compact fibrolamellar tissues and may have had some connection to the median pit since it is located near the midline.

A number of cracks radiate through ISIR 268, one of which appears to correspond with the zipper-like, frontal-parietal suture, as can be seen at the location where the suture (yellow line) terminates on the anterodorsal surface (Figure 13a).

2.6 | Histology discussion

In mammals, most cranial expansion of the skull roof occurs in the diploe, the spongy layer sandwiched between the endocranial and exocranial tables of the intramembranous calvarium (e.g., Farke, 2010; Kulik & Sidor, 2019). In reptiles, including birds, there is nothing to suggest that the situation is any different. The expansion of any cranial element that borders the endocranium is, by definition, a widening of the space between the ventrally facing roof of the brain case and the exterior roof of the skull. The pachyostotic dome of *Kranosaura kuttyi* initially grew radially from the calvarial tissues above the braincase. As the skull grew, the median pit would have existed as an opening that deepened as the dome expanded. The walls of the pit were lined with periosteal tissues. Shortly after the inflation began, the radial orientation in the anterior region shifted slightly to expand the structure anteriorly as well as dorsally. This slight shift would eventually create the convex rostral face of the dome. The last shift in radial orientation occurred much later when the trabeculae shifted dorsoventrally, as can be seen in the posterodorsal portion of the dome (Figure10b,c; Figures 11a and 13a).

A dorsoventrally-oriented, tripartite histological zonation as described previously in pachycephalosaurs and burnetiamorphs, and suggested to exist in *Tropticus primus* (Stocker et al., 2016, Figure 2j,k) is not expressed in *Kranosaura kuttyi*, unless we consider these zones to simply represent the three layers of the typical calvarium. On the other hand, a slightly askew anteroposterior zonation is very evident in *K. kuttyi* described in this study. The fact that there is no evidence of osteoclast resorption or trabecular remodeling in any of the cancellous or dense regions indicates that the transitional trabecular spacing of coarse posteriorly to fine anteriorly was established as the dome expanded dorsally, or more accurately, dorsoventrally. The veneering of the trabeculae was the final stage in bone development prior to the death of the individual.

We hypothesize that the frontal-parietal suture originates as a wedge-shaped structure in the endocranial bone barrier between the braincase and ventral end of the median pit. The suture apparently continues up the anterior side of the median pit sagittally, or between Zones 1 and 3 laterally, for nearly 2/3 the height of the dome before arcing anteriorly to terminate with the exterior surface of the dome. Interestingly, what we hypothesize to be the parietal cap of *K. kuttyi* is composed almost exclusively of woven trabeculae lacking both lamellar veneering and any orientation. The woven isotropic tissues indicate that the collagen fibers are totally unorganized, a characteristic typical of embryonic bone. It is very likely that this region of the dorsal cap of the skull would have been highly vulnerable to damage from head-to-head contact. The rostral face of the dome; however, is composed of dense, mature fibrolamellar bone that was more likely highly resistant to stress, and indicates that these animals could have used the convex anterior wall of the dome of their skulls for some type of display activity. Both the apparent delicate parietal cap and strengthened rostral face are unique characteristics of the *K. kuttyi* dome and unlike any other previously described dome-headed animal.

The anomalous area in the posteroventral region of the skull in ISIR 268 is of particular interest because of its proximity to the dural peak of the braincase. It is unusual to have an island of simple, fibrolamellar tissues bordered by more mature tissues unless it was deposited much later ontogenetically than the adjacent tissues. If this were the case, there would have been a vacuity that extended from near the posterior base of the dorsal pit nearly to the anterodorsal edge of the dural peak of the braincase. The same region is not easily observed in *Triopticus primus*, but CT data of this region (Figure 9e,f) suggest a similar configuration; if there was a connection between the dorsal pit and the endocranial cavity, it would occur at the posteroventral end of the dorsal pit at the anterodorsal edge of the dural peak.

3 | DISCUSSION

3.1 | Phylogenetic relationships

The much more complete skull of *Triopticus primus* was previously coded into an archosauromorph phylogenetic matrix (Stocker et al., 2016), and the taxon is recovered as a stem archosaur near the divergence of Archosauria. The phylogenetic position among non-archosaurian archosauriforms is not strong, and the placement in this part of the tree is a minimum phylogenetic position. The presence of an antorbital fenestra and fossa based on the morphology of the lacrimal, as well as the presence of an ossified laterosphenoid, drive much of the phylogenetic placement among non-archosaurian archosauriforms.

Kranosaura kuttyi and *Triopticus primus* possess a suite of character states that demonstrate a close relationship (see diagnosis), but their relationship to other reptiles remains mired given the highly unique skulls of both taxa combined with the lack of other parts of the skeleton. This is further complicated by the lack of new character observations in both specimens of *Kranosaura kuttyi*. *Kranosaura kuttyi* had identical character state scores as *Triopticus primus* and no other characters were scored in *K. kuttyi* that were not already scored in *T. primus*.

3.2 | Taphonomy and preservation

The pitting observed on the anterodorsal frontal region of the holotype (ISIR 269) and the referred specimen (ISIR 268) of *Kranosaura kuttyi* bears an outward resemblance to the pits and pores observed in ontogenetically younger individuals of *Stegoceras validum* (Schott et al., 2011: Figure 3), assorted frontoparietal domes of *Stegoceras edmontonense* (Giffin, 1989: Figure 5), *Colepiocephale lambei* (Schott et al., 2009: Figure 2), *Sphaerotholus goodwini* (sensu Williamson & Carr, 2002; Figure 1), and other pachycephalosaurs (Sullivan, 2006: Figures 4 and 5). The accompanying sulci or grooves surrounding many of these pits, referred to as a 'tesserate' pattern in some pachycephalosaur studies (Schott et al., 2009; Williamson & Carr, 2002), are present in ISIR 268 (see Figure 3a), but the grooves normally surrounding the pits are less visible in ISIR 269 (see Figure 2a). A reduction in the depth and overall absence of these grooves or sulci occurs in the relatively smoother frontoparietal domes of ontogenetically older pachycephalosaurs (Goodwin & Horner, 2004), particularly in *Pachycephalosaurus* (Horner & Goodwin, 2009). One hypothesis is that individual keratinous plates or scales responsible for the sulci coalesce ontogenetically resulting in the smoother dorsal surface of the dome observed in older individuals. Should this be the case, the referred specimen (ISIR 268) may be slightly younger ontogenetically than the holotype of *Kranosaura kuttyi* (ISIR 269). The presumed obliterated sutural morphology of ISIR 268 (Figure 11a) indicates it is likely a relatively mature individual.

3.3 | Pangean distribution

Members of Protopyknosia were broadly distributed in the early Late Triassic, with specimens known from both western North America and India (Figure 1), which belies the rarity of this new clade. The Otis Chalk localities were formed at approximately 10°N latitude in the equatorial belt of western Pangea, whereas the Upper Maleri Formation was deposited at approximately 30°S latitude on the eastern, Tethyan side of Pangea (Brusatte et al., 2013; Sellwood & Valdes, 2006). Both of these areas are hypothesized to have been within the 'summer wet' biome (Sellwood & Valdes, 2006) with monsoonal conditions. That a dome-headed representative of Protopyknosia has not been found in the well-sampled southwestern USA (e.g. Chinle Formation) supports that this clade was extremely rare and may have more to do with timing than with climate or geography.

Additionally, Protopyknosia appears to span biozones (Otischalkian to Adamanian). The Colorado City Formation, from which *Triopticus* is known, is the basis for the Otischalkian biozone, based on the presence of *Parasuchus* (Lucas & Hunt, 1993; Kammerer et al., 2016; Martz & Parker, 2017; Beyl et al., 2020), in addition to metoposaurid temnospondyls, desmatosuchinine aetosaurs, the dinosauromorph *Dromomeron gregorii*, and dinosaurs (Elder, 1978; Stocker et al., 2016). These localities are interpreted to be latest Carnian to earliest Norian (227–224 million years ago) based on vertebrate biochronology and lithostratigraphic correlations with U-Pb geochronology from the Chinle Formation of Arizona (Atchley et al., 2013; Chatterjee, 1978; Elder, 1978; Martz, 2008; Martz & Parker, 2017; Ramezani et al., 2014; Stocker et al., 2016). Support for a Carnian age for the Otis Chalk localities is weak, though not negative, because of the reassessment of '*Francosuchus*' *trauthi* (=*Dolerosaurus trauthi*) from the Carnian marls of the Opponitzer Limestone of the upper Lunz Formation (Late Triassic, Tuvalian) as a probable non-phytosaur (Butler, 2013). Radioisotopic dates for portions of the Chinle Formation, however (e.g., Irmis et al., 2011; Ramezani et al., 2014), indicated that exposures of the Chinle Formation in Arizona and New Mexico are entirely post-Carnian (Irmis et al., 2011; Olsen et al., 2011). Other Otischalkian units include the Popo Agie Formation of Wyoming (Lucas & Hunt, 1993; Stocker, 2013), which has not had the same intensity of sampling as the Chinle Formation or Dockum Group and may later be found to preserve a *Triopticus*-like taxon, though no diagnostic skull material of this clade is currently known from the Popo Agie.

In contrast, though the neotype of *Parasuchus* is from the Lower Maleri Formation (Chatterjee, 1978), the Upper Maleri Formation (Chatterjee, 1987; Novas et al., 2011), from which *Kranosaura* is known, is reported to preserve 'advanced phytosaurs' (see Locality and Age above; Chatterjee, 1986; Hungerbühler et al., 2002) and chigutisaurid amphibians (e.g. Novas et al., 2011). Those phytosaurs were reported to be similar to *Rutiodon*/*Angistorhinus* and *Leptosuchus* and be Norian (post-Ischigualastian; Langer, 2005) in age. In North America, the leptosuchomorph phytosaur *Smilosuchus* is one of the taxa that are characteristic of the Norian-aged Adamanian biozone (Martz & Parker, 2017; Parker & Martz, 2011). Additionally, the presence of chigutisaurid temnospondyl amphibians indicates a post-Ischigualastian age (Langer, 2005). Therefore, members of Protopyknosia are present in both the Otischalkian and Adamanian biozones and may have been present from approximately 227 to 215 Ma.

3.4 | Convergence with other boneheads

Convergent morphologies across vastly diverse lineages was highlighted for archosauriforms with the initial description of *Triopticus primus* from the Late Triassic Otis Chalk localities (Stocker et al., 2016) and extended further with the discoveries of the archosauromorph *Shringasaurus indicus* (Sengupta et al., 2017) with ceratopsian-like horns above the orbits and *Eretmorhipis carrolldongi* (Chen et al., 2015; Cheng et al., 2019) resembling the platypus in cranial morphology. The outward similarity of *Triopticus*, and now by extension *Kranosaura*, to pachycephalosaurid dinosaurs was centered on the incompletely preserved skull roof of the holotype material. In both cases, the frontal region is dorsally expanded into a dome-like structure and this expansion also expands posteriorly to overhang the braincase area as in pachycephalosaurid. Among amniotes, generally similar dorsal expansions of the skull are present in synapsids (e.g., tapinocephalids and biarmosuchians; Kulik & Sidor, 2019) and it was recently shown by Kulik and Sidor (2019) that growth of biarmosuchians expansions were markedly different than that of pachycephalosaurid dinosaurs. Similarly, we show that with deeper exploration of the cranial histology of *Kranosaura*, a member of Archosauromorpha like that of pachycephalosaurids, reveals that any similarity between members of Protokypnosia and pachycephalosaurids is indeed mainly skin deep.

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AUTHOR CONTRIBUTIONS

SJN: Designed and conducted research, wrote paper, assembled figures; MRS: Designed and conducted research, wrote paper, assembled figures; SC: Provided the ISI specimens, designed and conducted research, wrote paper; JRH: Designed and conducted research, described the histology, wrote paper, assembled figures; MBG: Designed and conducted research, discussed the histology, wrote paper.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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